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27 Abstract

Laboratory and field studies were conducted to evaluate the importance of periphyton in western Lake Superior with special reference to the make-up and distribution of the periphyton growths and to the overall importance of productive capacity of this assemblage of organisms. The taxonomic portion of the investigation indicated that over 90% of the total number of organisms were diatoms and that the phyla to which these diatoms belonged were the Chrysophyta, the Chlorophyta, and the Cyanophyta. Predominant genera were Synedra, Achnanthes, Navicula, Cymbella, and Gomphonema. In many respects, the periphyton of Lake Superior was similar to that found in streams and there was evidence that the interrelated factors that affected periphyton growths were temperature, light intensity, depth of water, water movements, nutrient levels, and the type of substrate. Artificially denuded rocks demonstrated definite re-growth but after 46 days this growth level was only 18% of that occurring naturally. The mean total counts of organisms in the primary sampling area ranged from 497,000 to 1,470,000 per square centimeter of rock surface. Studies of the pigment concentrations showed that the biomass of periphyton along the North Shore of Lake Superior resemble those of other oligotrophic bodies of water and range from 0.338 to 3.59 mg of total pigment per 100 square centimeters of rock surface. The average was 1.36 mg per 100 square centimeters of rock surface. Pigment ratios indicated that the Lake Superior periphyton was dominated by the Chrysophyta.

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Abstract (continued)

Assimilation values for Stony Point Bay averaged 1.48 grams of carbon fixed per gram of chlorophyll in 1967. In Stony Point Bay, the total standing crop in terms of dry weight was 55.5 tons. In re-growth studies, chlorophyll levels were observed to increase by an average of 0.057 grams (57 mgs) per square meter per day. The efficiency of energy utilization in Stony Point Bay was found to be 0.082%, a typical value for algal communities.

(T.O. Olson and T. O. Odlaug) University of Minnesota

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LAKE SUPERIOR PERIPHYTON
IN RELATION TO WATER QUALITY

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ABSTRACT

Laboratory and field studies were conducted to evaluate the importance of periphyton in western Lake Superior with special reference to the make-up and distribution of the periphyton growths and to the overall importance of productive capacity of this assemblage of organisms.

The taxonomic portion of the investigation indicated that over 90% of the total number of organisms were diatoms and that the phyla to which these diatoms belonged were the Chrysophyta, the Chlorophyta, and the Cyanophyta. Predominant genera were Synedra, Achnanthes, Navicula, Cymbella, and Gomphonema.

In many respects, the periphyton of Lake Superior was similar to that found in streams and there was evidence that the interrelated factors that affected periphyton growths were temperature, light intensity, depth of water, water movements, nutrient levels, and the type of substrate.

Artificially denuded rocks demonstrated definite re-growth but after 46 days this growth level was only 18% of that occurring naturally.

The mean total counts of organisms in the primary sampling area ranged from 497,000 to 1,470,000 per square centimeter of rock surface.

Studies of the pigment concentrations showed that the biomass of periphyton along the North Shore of Lake Superior resemble those of other oligotrophic bodies of water and range from 0.338 to 3.59 mg of total pigment per 100 square centimeters of rock surface. The average was 1.36 mg per 100 square centimeters of rock surface. Pigment ratios indicated that the Lake Superior periphyton was dominated by the Chrysophyta. Assimilation values for Stony Point Bay averaged 1.48 grams of carbon fixed per gram of chlorophyll in 1967. In Stony Point Bay, the total standing crop in terms of dry weight was 55.5 tons.

In re-growth studies, chlorophyll levels were observed to increase by an average of 0.057 grams (57 mgs) per square meter per day.

The efficiency of energy utilization in Stony Point Bay was found to be 0.082%, a typical value for algal communities.

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SECTION I

CONCLUSIONS

A. Periphyton Taxonomy and Distribution

(1) The plant portion of the periphyton found attached to rocks consisted almost entirely of representatives from three phyla of algae, namely the *Chrysophyta*, the *Chlorophyta*, and the *Cyanophyta*.

(2) The genera of diatoms which were predominant in the periphyton growth were *Synedra*, *Achnanthes*, *Navicula*, *Cymbella*, and *Gomphonema*.

(3) The periphyton of Lake Superior was found to be similar, in many respects, to attached growths found in streams.

(4) The interrelated factors which affect periphyton growth are light intensity, water movement, temperature, water depth, water movement, nutrient levels, and type of substratum.

(5) Most abundant in terms of numbers of organisms was the phylum Chrysophyta, and diatoms made up over 90% of this group.

(6) Mean total counts of organisms in the naturally occurring periphyton of Stony Point Bay, the primary sampling area, ranged from 497,000 per square centimeter of rock in 1966 to 1,470,000 in 1967.

(7) The biomass of the naturally occurring Stony Point Bay periphyton in terms of dry weight, was 153 grams per square meter in 1965, 104 gr/m^2 in 1966, and 156 gr/m^2 in 1967.

(8) After 46 days of regrowth on artificially denuded rocks, the growth level finally reached was approximately 18% of that occurring naturally.

(9) The daily regrowth production rate in Stony Point Bay averaged 3.6 grams of dry weight per square meter and 0.067 grams of organic weight (ash-free dry) per square meter.

(10) Mean total counts of organisms from eleven North Shore stations ranged from 1,466,000 organisms per square centimeter at Sugar Loaf Cove to 3,798,000 per square centimeter at Split Rock River Bay.

B. Periphyton Pigments and Productivity

(1) Pigment concentrations showed that the biomass of the periphy-

ton of Lake Superior's North Shore was similar in magnitude to other oligotrophic bodies of water. Total pigment concentrations ranged from 0.338 to 3.59 milligrams per 100 square centimeters of rock surface, and averaged 1.36 mg/100 cm^2.

(2) Pigment ratios indicated that most of the North Shore periphyton was dominated by organisms of the Phylum Chrysophyta.

(3) Assimilation values for Stony Point Bay periphyton averaged 1.48 grams of carbon fixed per gram of chlorophyll in 1967.

(4) The total standing crop of Stony Point Bay periphyton in terms of dry weight was 55.5 tons, or 156 grams per square meter in 1967.

(5) Regrowth periphyton over a period of 46 days was equivalent to approximately one-third only of the biomass of naturally occurring periphyton. Chlorophyll levels increased by an average of 0.00057 grams per square meter per day.

(6) Net production by the periphyton in 1967 averaged 1.01 grams C fixed/M^2/day or 3.35 grams glucose per M^2/day. The ratio of gross photosynthesis to respiration averaged 3.17.

(7) In water up to 40 feet deep in western Lake Superior periphyton can be five to six times as important in primary production as the phytoplankton.

(8) Laboratory experiments showed that alteration of light intensity (below 800 foot-candles) caused a rapid change in the chlorophyll content of the periphyton. The maximum rate of chlorophyll reduction in response to a substantial increase in light intensity was shown to be 12.7 per cent per day for eight days. The most rapid increase in chlorophyll concentration in response to a severe reduction in light intensity was 7.5 per cent for six days.

(9) Short-term "conditioning" of periphyton to different combinations of light intensity and temperature caused a variety of responses when the photosynthetic rate was measured in crossed gradients of light intensity and temperature.

(10) For conditioned samples at light saturation Q_{10} ranged from 1.24 to 2.48. The compensation point varied from 80 to 130 foot-candles.

(11) Naturally occurring periphyton was shown to exhibit typical "light-adapted" or "shade-adapted" photosynthetic reaction depending on the prevailing level of light intensity.

(12) The efficiency of energy utilization by Stony Point Bay periphyton was found to be 0.82 per cent, a typical value for algal communities.

SECTION II

RECOMMENDATIONS

The study which has been carried out has opened up a number of avenues which should be explored if the future welfare of Lake Superior is to be kept in mind:

(1) What role, if any, does the periphyton play in the transfer of energy to the second trophic level?

(2) Do any animals actually feed directly on Lake Superior periphyton?

(3) What is the general level and seasonal variation of phaeophyton in naturally occurring periphyton at various depths?

(4) What are the effects of increased nutrient concentrations and increased temperature on the periphyton?

(5) Is periphyton a source of phytoplankton?

(6) How much time is required for regrowth periphyton to reach the level of naturally occurring biomass?

(7) What is the level of radioactivity in the periphyton mass? The answer to this question would be of particular interest should a nuclear-fueled power plant be located on the North Shore of Lake Superior.

SECTION III

INTRODUCTION

Lake Superior, with a surface area of 31,820 square miles, is the largest body of fresh water on earth. It lies at the head of the chain of Great Lakes which include, in addition to Lake Superior, Lake Michigan, Lake Huron, Lake Erie and Lake Ontario. Lake Superior is 350 miles long with a maximum breadth of 160 miles. It lies 602 feet above sea level and has a maximum depth of 1333 feet.

Lake Superior, despite its vast size and relatively dramatic formation, is in many ways ecologically similar to a one-half acre farm pond. Both bodies of water, for instance, depend upon the sun as their original energy source and, through a complex series of energy transfers, maintain their own characteristic ecosystem. To accomplish this, both require populations of algae, which Gilbert M. Smith (1933) defines as "simple plants with an autotrophic mode of nutrition". In an aquatic environment, algae may be either attached or free-floating. When algae are attached to aquatic plants or other surfaces projecting above the bottom, they constitute a part of the periphyton. Free-floating algae are known collectively as phytoplankton and along with minute organisms such as rotifers and crustaceans, called zooplankton, constitute the plankton. The latter term may be defined as the assemblage of microscopic or near-microscopic plants and animals which are non-motile or weakly motile and whose transport is, therefore, dependent upon the wind, waves, or current.

Since algae are ubiquitous in the euphotic zone of a body of water, their available habitats are almost endless, as are the descriptive terms applied to them. For example, when algae are found at the air-water interface, they are part of the neuston. In beach sand, they would be referred to as psammon. When periphyton algae break loose from their substratum and are found unattached as a part of the phytoplankton, they become tychoplankton. Wherever they occur, their primary function is the photosynthetic fixation of carbon. By this process of photosynthesis, algae produce organic matter from basic inorganic components and may, therefore, be referred to as primary producers. As such, they form the first link in the aquatic food chain.

Algae, regardless of their habitat, are fed upon by consumers (heterotrophs), such as zooplankton and immature insects. These forms are fed upon by small fish which, in turn, may be eaten by larger fish. Ultimately, the larger fish may be fed upon by man. Each group of consumers has a definite position, or trophic level, in the so-called food pyramid. Ecologists have long used this concept. It was originally proposed by Charles Elton in 1927 as a simple graphic representation of the food chain or web. Producer organisms constitute the base of the Eltonian pyramid, consumers the remainder. Each successive tier,

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in units of biomass, numbers, or energy, becomes smaller and smaller. At the apex one finds man, or some other dominant carnivorous species. The precise organisms, of course, will depend on the ecosystem under scrutiny.

In addition to the free-floating or attached organisms mentioned above, producers and consumers may also be found in or on the bottom. The animals usually feed upon settled or settling organic debris and consist of forms such as nematodes, annelids, protozoans, molluscs, et cetera. The plants, consisting chiefly of algae, grow as a thin layer on the surface of the sediment.

For the proper functioning of an ecological community, organisms other than producers and consumers are needed. These are the decomposers, which consist primarily of bacteria and fungi. Such organisms are found in all habitats. Their function consists of breaking down organic matter, usually in the form of dead animals and plants, into their inorganic constituents so that they may be utilized once again by the autotrophs.

Thus, it can be seen that algae, in both the periphyton and the plankton, are the fundamental units of any aquatic environment. Lake Superior, with its approximately three thousand cubic miles of water, supports vast quantities of phytoplankton. However, its irregular shoreline area, which is even larger than the lake's breadth and width would suggest, is virtually completely covered by periphyton. While water from the open lake must be concentrated before the phytoplankton can be counted, periphyton scraped from a small rock must be diluted before a satisfactory count can be made. Periphyton organisms, due to their need for light, are most abundant near the shore. Here they are washed by shore currents and water movements induced by wind. In view of this constant exposure to ever-changing masses of water, this community should reflect certain characteristics of the lake, particularly the quality of the water. In the report which follows, this important component of the biota of Lake Superior will be defined qualitatively as well as quantitatively. In addition, certain ecological aspects of the periphyton and its possible role in the economy of Lake Superior will be considered.

Although periphyton has been briefly defined in the preceding description of an aquatic ecosystem, the confusion that exists in the literature over the precise meaning of this term points out the need for a more exact definition. Alena Sladeckova (1962), in her excellent monograph on the investigation of the periphyton community, discusses in some detail the terminology of this attached, aquatic association. Our use of the term "periphyton" follows the generally accepted definition proposed by Young (1945) and quoted by Sladeckova and Welch (1948).

> "By periphyton is meant that assemblage of organisms growing upon free surfaces of submerged objects in water, and covering them with a slimy coat. It is that slippery brown or

green layer usually found adhering to the surfaces of water plants, wood, stones, or certain other objects immersed in water and may gradually develop from a few tiny gelatinous plants to culminate in a wooly, felted coat that may be slippery, or crusty with contained marl or sand."

The German word "aufwuchs" may be considered essentially synonymous with Young's definition of periphyton. Ruttner (1963) defines "aufwuchs" as those organisms that are firmly attached to a substrate but do not penetrate into it." As the translator (Frey and Fry) of Ruttner's text point out, the term "aufwuchs" has a broader connotation than does the term periphyton as used by some English-speaking authors. Prescott (1957), for example, defines periphyton as "organisms which form associations on the stems and leaves of aquatic plants." "Aufwuchs", as delineated by Ruttner, includes all the attached organisms except the macrophytes, as well as the unattached forms living free within the mat of attached organisms. Up to this point, "aufwuchs" and Young's definition of periphyton are synonymous. Ruttner's definition of "aufwuchs", however, does not contain the word aquatic. "Aufwuchs" may, therefore, exist in a terrestrial habitat with an adequate moisture content while periphyton, as defined by Young, is necessarily aquatic. With this exception, periphyton and "aufwuchs" are synonyms. Other authors prefer not to use either term and refer to this community as benthic algae (Blum, 1956 and Round, 1964), benthos (Lund and Talling, 1957), or other similar terms. However, the terms "benthos" or "benthic" usually refer to those unattacked organisms living in or on the bottom sediments.

Strictly speaking, periphyton includes both plants and animals. Although the previously cited definitions use only the work "organisms", Odum (1959) defines periphyton as "organisms (both plant and animal) attached or clinging to stems or leaves of rooted plants or other surfaces projecting above the bottom." The vast majority of the periphyton community, however, is composed of plant material. This investigation, therefore, deals only with the members of the periphyton belonging to the plant kingdom. The term "epilithic", as used in this report, refers to the fact that the periphyton studied was growing upon rocks.

In his book on the algae of the western Great Lakes area, G. W. Prescott (1962) states that "although convenient, the term algae has been applied to such a great variety of plant groups and has been given so many interpretations that it has no very precise meaning." It is not surprising, therefore, that basic algal taxonomy has long been, and remains, a subject of controversy among botanists. The details of algal taxonomy, therefore, will depend upon the authority consulted. Fuller and Tippo, in their 1949 textbook, for example, divide the algae into seven separate phyla under the subkingdom Thallophyta. Prescott (1962) solves the problem of taxonomy in a somewhat similar fashion, placing the algae in eight phyla, or divisions, as he calls them. Robbins, Weier, and Stocking (1967) suggest six phyla, with the blue-green algae included in the phylum Schizophyta along with the bacteria, class Schizomycetes. G. M. Smith (1933), on the other hand, divided the algae into nine classes under the phylum Thallophta. In 1950, he reorganized his algal groupings and raised most of the classes to division (phylum) status. This resulted in seven divisions. For reasons of simplicity, we have adopted in this report the conservative taxonomic system proposed by Fuller and Tippo (1949), whose seven phyla are, for practical purposes, identical to those of Smith (1950).

The productivity of a periphyton or plankton community may be measured by either of two general methods, each with its own special applicability. One is the evaluation of the "standing crop", or the determination of biomass, which is quite significant when attention is paid to the rate of establishment and "turnover" of the communities. The other method involves the investigation of the dynamics of energy transfer through the communities, or more specifically, the determination of photosynthetic rates. The estimation of "standing crop" may include taxonomic studies, the determination of numbers of organisms, the measurement of weight or volume of the communities, or the quantitative analysis of some component of the organisms, such as carbon, nitrogen, photosynthetic pigments, or DNA. The measurement of photosynthetic and respiratory rates may be used to calculate gross primary productivity (the total rate of photosynthesis including the organic matter used up in respiration) and net primary productivity (the rate of storage of organic matter in plant tissues in excess of respiratory utilization). The latter may also be termed "apparent photosynthesis" or "net assimilation." When both "standing crop" and assimilation rates for all communities of primary producers have been determined the true basic productivity of an ecosystem may be calculated.

The overall objective of the study being reported here is to fill in some of the gaps of knowledge relating to periphyton in general. Specifically, it will deal with the characteristics of naturally occurring periphyton growths in a relatively unpolluted and very large body of fresh water, the western arm of Lake Superior. Although the future role of Lake Superior in the overall water economy of this continent cannot be exactly predicted, it is generally agreed that any change that occurs in this large body of water will have important and far-reaching effects on the entire "heart-land" of America. Therefore, it may be expected that a consideration of the periphyton and its importance as a part of the ecosystem will provide data on the general character of the lake which can be used as a reference or base-line in future years to estimate tendencies toward eutrophication. The rationale involved in this concept, fixed as it is in a region of the lake where it is constantly swept by waves and currents, might be expected to develop in ways which would reflect the characteristics of the water.

Specifically the study was directed toward the determination of:

1. The extent of natural periphyton growths in certain selected areas of Lake Superior, quantitatively determined.

2. The make-up of the periphyton mass in terms of its animal and plant components with special attention to the algae, a taxonomic analysis.

3. The speed and the phases of growth demonstrated by periphyton in re-establishing itself on an artificially denuded substrate.

4. The primary productivity potential of the periphyton and its relation to the typical productivity of the water in the open lake.

5. The possible interrelationship existing between plankton and periphyton.

6. A study of the nature of the photosynthetic pigments and their relationship to environmental factors such as depth and light.

The measurement of photosynthetic pigments has been long recognized as a fast and relatively easy method for estimating the productivity of plankton populations. According to Richards and Thompson (1952), the analysis of plankton pigments, when extended to include the various chlorophylls and carotenoids, should yield "(a) a measure of the potential of the plankton for absorbing radiant energy for photosynthesis, (b) some measure of the extent and stage of development of the phytoplankton, and (c) a possible measure of the presence of animals grazing on the crop". The relative concentrations of chlorophylls a, b and c also reflect to a certain degree the composition of an algal community, since members of the various phyla contain different ratios of these pigments. The use of pigment analysis can logically be extended to the determination of the standing crop of epilithic periphyton, and further, to the estimation of the rate of carbon fixation, when assimilation values are known or assumed.

SECTION IV

MATERIALS AND METHODS

A. Occurrence, Regrowth, and Taxonomy of Periphyton

The area from which the majority of samples were obtained was a small bay at the western end of Lake Superior which is known locally as Stony Point Bay (Figs 1 & 2). It is situated approximately fifteen miles northeast of the Duluth, Minnesota city limits and University of Minnesota Limnological Research Laboratory at Lester River. Lying two miles south of Knife River Harbor, where the thirty-foot motorized research vessel, the Oneota, is moored, the study area is bounded by the Little Sucker River on the southwest and Rocky Point on the northeast.

The investigations began during the summer of 1965 (July 19 - September 1) with a general survey of the study area. Conventional surveying techniques were employed, utilizing a baseline, stadia readings and a professional transit. For the purpose of establishing the contour of the shoreline of the bay, a base station was selected in the approximate center of the arc formed by the water's edge. This base station was located directly below a tourist observation point on a hill above the bay. A line, which extended from this station to a point on the shoreline 427 ft. away at an angle of 84°30' east of south, was then established. The transit was used to determine the angle of this baseline while a stadia rod was employed to ascertain the distance. Points along the shoreline from the Little Sucker River to Rocky Point were then marked with fluorescent paint. The exact position of each of these marked points with relation to the baseline was determined by triangulation and plotted on the master map, thus providing an accurate delineation of the water margin.

The second phase of the survey was the determination of the depth profile of the bay. The Oneota was used to place an initial reference buoy at a point 2336 feet from shore and in a southerly direction from the establihsed base station. With the stadia rod aboard the boat and the transit ashore, it was possible, by knowing the distance of the vessel from shore and its angle from the base station, to determine the exact position of the Oneota at each sounding. Depth readings were made with an electric fathometer. At the depths encountered, the instrument was accurate to within six inches. Depth readings were relayed to shore by hand signals so that each depth determination could be related to the position of the boat as it traversed the bay.

When depth permitted, the type of bottom was determined by water glass observations. When the water was too deep for this procedure, SCUBA-diving procedures were employed to ascertain the bottom type.

A small dinghy was used to survey shallow areas less than ten

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feet in depth. The Oneota could not be used here due to the presence of occasional protruding boulders. The position of the dinghy at each depth reading was determined by the triangulation method used to locate the larger boat. Depth readings from the dinghy were made with a marked sounding pole. A water glass or simple visual observation was used to determine the type of bottom. The depths established by these procedures were then plotted on the master map. Points of the same depth were connected, thus providing a depth contour. Intermediate depths were established by interpolation. These contours are included in the map of the bay which also indicates the type of bottom. The bottom area not designated by the word sand was covered with rocks. It should be pointed out that small sand patches were encountered in predominantly rocky areas while the sand patch contained small areas of rock bottom.

In sampling, an imaginary line extending from the reference buoy 2336 feet from shore to the base station was used for orientation. Whenever possible, samples were collected along this line. The same line was used for the placement of the rocks used in the regrowth studies.

The study began during the summer of 1965 with an evaluation of the regrowth capabilities and the taxonomy of the periphyton. This was a qualitative study. The substrata chosen for the regrowth study were rocks already present and supporting periphyton growth in Stony Point Bay. By choosing these rocks, we hoped to minimize any deviations from the naturally occurring periphyton populations that might occur if rocks foreign to the area were used as substrata. Artificial substrata were not used for the same reason. In addition, unpublished preliminary studies made by Olson and Odlaug in which glass slides, tile, fish net, wood, and other materials were used, showed that the type of substratum material affected periphyton growth. For the regrowth studies, therefore, medium-sized rocks (eight to twelve inches in diameter) were taken from shallow water in the bay and returned to the laboratory in plastic buckets. There the rocks were thoroughly scrubbed with a stiff-bristled plastic fingernail brush and rinsed with tap water. A three-eighths inch wooden dowel was driven into the hole. The rocks, with attached pegs, were then autoclaved at fifteen pounds per square inch (250°F.) for twenty minutes and after sterilization, were replaced in the lake. The rocks were lowered to the bottom by ropes attached to the pegs at designated stations and depths. Styrofoam buoys attached to the ropes marked the locations of the rocks. In water depths greater than ten feet, SCUBA diving techniques were employed to determine the nature of the bottom and to make sure that the experimental rocks were in a suitable position for regrowth to occur.

After an "incubation" period which ranged from three to twenty-seven days, the rocks were retrieved by slowly pulling them back up by the buoy ropes. This simplified technique was permissible because this was a preliminary qualitative study. At the surface, the rocks

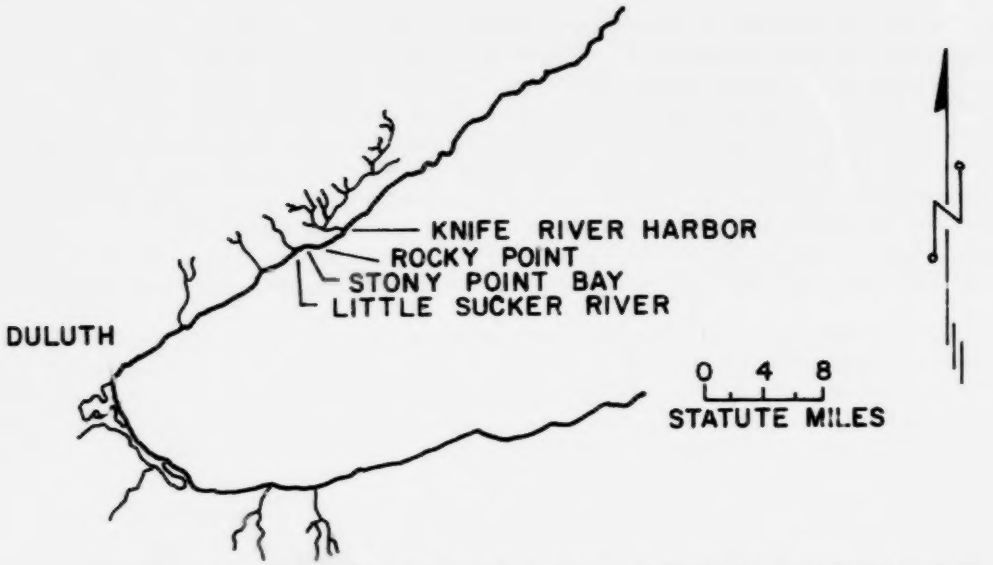
KNIFE RIVER HARBOR
ROCKY POINT
STONY POINT BAY
LITTLE SUCKER RIVER
DULUTH
0 4 8
STATUTE MILES

FIGURE I. WESTERN ARM OF LAKE SUPERIOR, SHOWING THE POSITION OF STONY POINT BAY, SITE OF PERIPHYTON STUDIES.

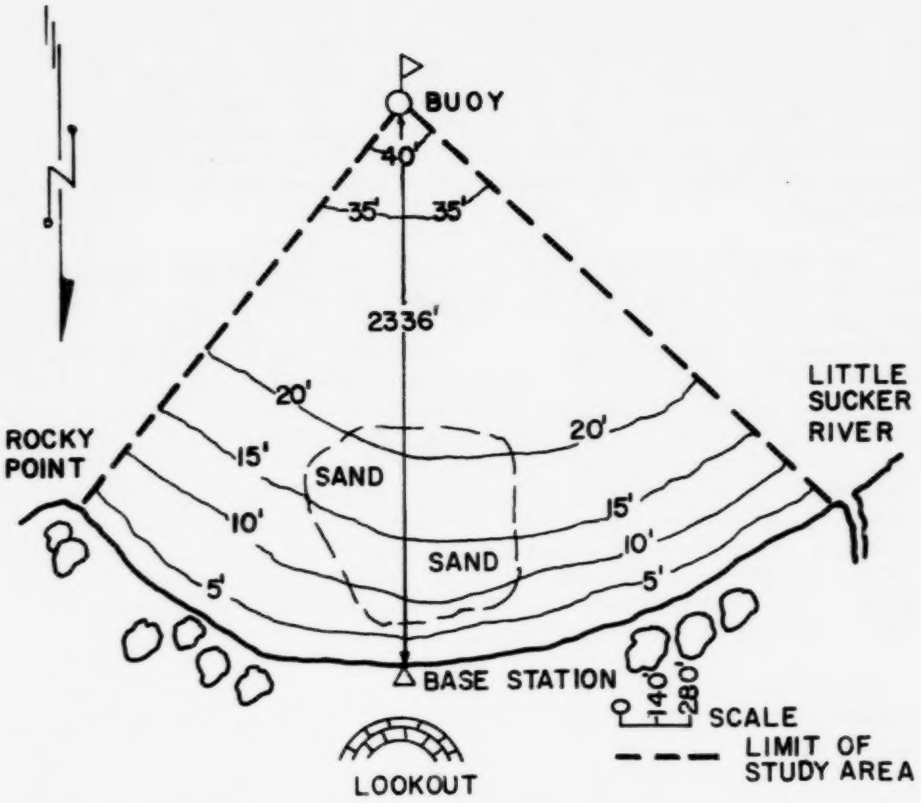
BUOY
40'
35'
35'
2336'
20'
20'
15'
15'
10'
10'
5'
5'
SAND
SAND
ROCKY POINT
LITTLE SUCKER RIVER
BASE STATION
0 140' 280'
SCALE
LIMIT OF STUDY AREA
LOOKOUT

FIGURE 2. DETAILED MAP OF STONY POINT BAY, LAKE SUPERIOR.

were carefully placed in individual plastic buckets which were then transported to the laboratory. There the rocks were scrubbed clean with a brush and rinsed with distilled water to remove the surface growth. A small funnel was then inverted in the periphyton-water suspension and rapidly moved in a vertical direction. During this thorough mixing, two fifty milliliter samples were removed by dipping. One of these samples was placed in a seventy-five milliliter amber bottle and preserved by bringing the aliquot to a five per cent formalin concentration. This aliquot was retained as a reference sample. The other remained unpreserved and was subjected to a prompt microscopic examination.

The microscopic examination was carried out at magnifications of 430 and 970 diameters. Drops of the sample were placed on a standard microscope slide and a standard square cover slip was used. Organisms were identified to genus and, when possible, to species. Each slide was examined until no "new" organisms were observed.

In addition to this microscopic examination of the regrowth periphyton, determinations were made of the dry weight of naturally occurring populations of periphyton. For this purpose, three rocks (four to six inches in diameter) were obtained at each of three depths. Waders were used to retrieve samples from the two foot depths near shore while rocks from depths of ten and twenty feet were obtained by SCUBA diving techniques. At these deeper depths, as determined by the fathometer aboard the Oneota, divers, each with his right hand and forearm in an inside-out clear plastic bag, reached out and grasped a sample rock with his right hand. With the left hadn, he then pulled the bag down over his forearm and hand, entrapping the sample rocks, as well as a small quantity of the surrounding water. The same plastic bag procedure was used at the two-foot depth. Each bag was knotted, brought to the surface and placed in a labelled plastic bucket with two other rocks from the same depth. The samples were returned to the laboratory within three hours.

At the laboratory, rocks were removed by slitting each bag open with a scalpel. Periphyton clinging to the bag was removed by rinsing with distilled water. The area on which growth occurred was marked by scraping an outline on each rock with a dull scalpel. Next, the periphyton was completely removed by scrubbing and rinsing with distilled water. The final sample from each depth consisted of the combined periphyton and rinse water from all three rocks. After each suspension of periphyton had been thoroughly agitated, using the funnel method described earlier, aliquots were removed, measured and filtered through Whatman filter paper. In order to insure a reasonable filtration time, the aliquot size was determined on the basis of the turbidity of each sample. In general, the sample sizes ranged from six to fifty milliliters. The filter papers were dried for one hour in an oven at 103°C., cooled in a desiccator and weighed.

In order to determine the extent of the surface upon which growth had occurred, the previously outlined area of each rock was lubricated with a thin layer of automobile grease and coated with paraffin. The paraffin was heated and applied with a paint brush until the rock was covered with a one-eighth to one-fourth inch coat. The wax was removed after it had solidified, but before it had become brittle, by cutting slits in the coating covering the vertical surfaces of the rock. The flaps created by these slits were then freed from the rock with a scalpel and the portion of the paraffin coat still attached to the horizontal surface was peeled off. By using this method, the coating could be removed as one intact piece. The paraffin was then gently pressed flat on a piece of white paper and its outline traced. A previously calibrated polar planimeter was used to determine the area enclosed by the tracing. Areas of the three rocks from each depth were combined.

During the summer of 1966 (August 9 - September 6), rocks were retrieved from depths of 2.5, 5, 10, 15, 20 and 35 feet. The depths of the deep water stations (ten feet and greater) were determined by the fathometer aboard the Oneota. Buoys were placed at these stations as permanent markers. The Oneota was used to transport divers and equipment to Stony Point Bay from Knife River Harbor and upon arrival at the bay, the vessel was anchored near the thirty-five foot buoy. Divers retrieved sample rocks using the plastic bag procedure earlier described. Again, three rocks were obtained from each depth. Laboratory procedures used for preparing the periphyton-water suspension followed those devised the previous summer.

A twenty-five milliliter aliquot to be used for counting, was removed and transferred to a seventy-five milliliter amber bottle. Twenty-five milliliters of ten percent formalin were then added. The mixture was thus preserved in five percent formalin and diluted twofold. A graduated dropper was used to transfer one milliliter of the sample into a Sedgwick-Rafter counting cell. After allowing ten minutes for settling, a binocular compound microscope was used to count ten random fields under a magnification of 200 diameters. The organisms were identified to genus. A Whipple disc, previously calibrated with a stage micrometer, was used to convert the ten random field counts into a count per milliliter. By knowing the total volume of the periphyton-water suspension, the dilution factor due to preservation and the rock area, it was possible to determine the number of organisms per square centimeter of rock surface. When the preserved sample was too turbid for accurate counting, an additional twofold dilution with distilled water was made.

For the determination of dry weights, a four milliliter sample was removed from the periphyton-water suspension, filtered through a pre-weighed Millipore membrane filter, dried for one hour in an oven at 103° C. and weighed. Results are expressed in milligrams per square centimeter of rock surface.

During the summer of 1967 (June 9 - September 15), the analysis of the naturally occurring periphyton in Stony Point Bay continued. A sampling run consisted of collecting three rocks from depths of 2.5, 5, 10, 15, 20 and 35 feet. At the time of each sampling run, light readings and water temperatures were taken. Light readings were made with a GM submersible photometer, which consists of two separate photometers, a deck and a sea cell. At the 35-foot station, readings were made at each meter from the water surface to the bottom. A standardized laboratory thermometer was used to determine the water temperature at the surface and at the bottom. A diver read the thermometer directly above the bottom at each sampling depth.

In addition to the studies of the naturally occurring periphyton of Stony Point Bay, denuded, autoclaved rocks were placed into the bay and retrieved at predetermined time intervals in order to quantitatively study the regrowth capabilities of the periphyton. Following the methods used during the summer of 1965, the rocks to be denuded and autoclaved were obtained by the use of waders from shallow, near-shore areas of Stony Point Bay. As described earlier, these rocks were returned to the laboratory where they were thoroughly scrubbed with brushes and autoclaved. Since this study was to be quantitative, the methods of necessity differed somewhat from those used the first summer. Instead of inserting pegs into the rocks and raising and lowering them in the lake by buoy lines, these rocks, after being lowered in a wire basket, were carefully placed in a circular configuration directly on the bottom. SCUBA divers placed the rocks at 10, 20, and 35 feet. A buoy marked each location. After the proper time interval had elapsed, three of the rocks were picked up by divers. The plastic bag technique was employed.

During the summer of 1967, samples of naturally occurring periphyton were collected from areas other than Stony Point Bay. A 107 mile segment of the north shore of the western arm of Lake Superior was sampled at intervals of approximately ten miles (Fig. 3). Beginning with the Lester River as the southernmost point, samples were collected as far north as Grand Marais, Minnesota. A fourteen-foot aluminum skiff with a five horsepower outboard motor was towed by car to each sampling location. Again, SCUBA diving procedures were used to collect three rocks from each depth sampled. The actual field techniques were the same as those used during the summer of 1966. Depths, however, were determined with a pitot-tube type depth gauge carried by the individual diver. These depth gauges had been calibrated against the electric fathometer aboard the *Oneota*. Temperatures were taken at the bottom and at the surface. Whenever possible, rocks were collected from each of the six standard sampling depths (2.5, 5, 10, 15, 20, and 35 feet) at each station. Each station was sampled on two different days. Collections were made at the locations shown below:

PERIPHYTON SAMPLING LOCATIONS, NORTH SHORE, LAKE SUPERIOR.

1.	LESTER RIVER	0 MILES
2.	KNIFE RIVER	13.8 MILES
3.	BURLINGTON BAY	22.1 MILES
4.	SPLIT ROCK RIVER BAY	39.4 MILES
5.	BEAVER BAY	48.0 MILES
6.	NO-NAME BAY	53.9 MILES
7.	SUGAR LOAF COVE	69.9 MILES
8.	TOFTE	78.8 MILES
9.	LUTSEN	86.3 MILES
10.	GOOD HARBOR BAY	100.9 MILES
11.	GRAND MARAIS	106.9 MILES

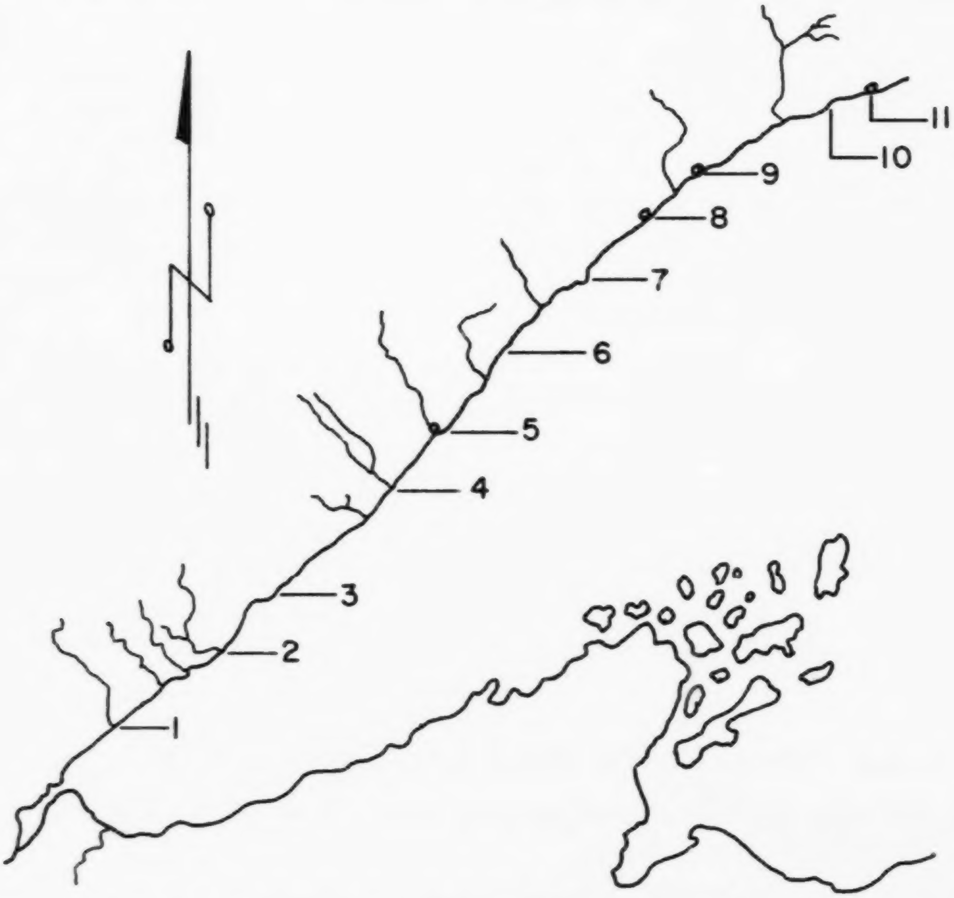

FIGURE 3. NORTH SHORE SAMPLING STATIONS AND THE WESTERN ARM OF LAKE SUPERIOR.

1.	Lester River	0 miles
2.	Knife River	13.8 miles
3.	Burlington Bay	22.1 miles
4.	Split Rock River Bay	39.4 miles
5.	Beaver Bay	48.0 miles
6.	No-Name Bay (near Little Marais)	53.9 miles
7.	Sugar Loaf Cove	69.9 miles
8.	Tofte	78.8 miles
9.	Lutsen	86.3 miles
10.	Good Harbor Bay	100.9 miles
11.	Grand Marais	106.9 miles

In the laboratory, all the rocks collected during 1967 were prepared for examination by the standard procedures adopted in 1966.

An aliquot consisting of 152 milliliters was removed for counting and identification. The sample was brought to a concentration of five percent formalin by adding eight milliliters of pure formalin. The counting procedure remained the same. Organisms were identified to genus and, when possible under a magnification of 200 diameters, to species. When samples were too turbid for examination, appropriate dilutions were made with distilled water.

After the counts were made, several drops of each sample were placed on a glass microscope slide which was then placed in a muffle furnace at 300° C. for ten minutes. After cooling, the ashed sample was covered with a glass cover slip, using Hyrax as the mounting medium. The ashing process incinerated all the material except the siliceous diatom frustules which were then examined microscopically under magnifications of 430 and 970 diameters. By using this procedure, many of the diatoms could be identified to species. These permanent diatom slides, from each depth and from each station, are now on file, as are the duplicate aliquots which were preserved in formalin.

For the determination of dry weights, twenty-five milliliter portions of the suspension were filtered through pre-weighed four-centimeter filter paper. Each filter was then placed in a weighed procelain crucible, dried for one hour in an oven at 103°C., cooled and reweighed. The samples were then ashed in a muffle furnace for fifteen minutes at 600°C. After cooling, they were again weighed in order to calculate ash-free (or organic) dry weights. Results are expressed as milligrams of total and ash-free weight per square centimeter of rock surface.

The remaining determinations, which included the pigment and the photosynthesis-respiration analyses, were made using the procedures of 1966.

B. Pigment, Productivity, and Physiology Studies of Periphyton

The first phase of the productivity study involved field studies in which the biomass, production rates and regrowth capabilities of naturally occurring periphyton in selected areas of Lake Superior were quantitated and analyzed on the basis of pigment concentrations, photosynthetic rates, and other parameters. The second phase was a laboratory study in which the effects of light intensity and temperature on pigment concentrations and photosynthetic rates of periphyton were determined experimentally. Most of the samples for both phases of the investigation were taken from a selected area within the confines of Stony Point Bay. This bay, as pointed out earlier, is situated on the western arm of Lake Superior near Duluth, Minnesota, fifteen miles northeast of the University of Minnesota Limnological Research Station at Lester River. The northeastern boundary of the study area is Stony Point, while the mouth of the Little Sucker River serves as the southwestern boundary. Two miles to the north is Knife River Harbor where the research vessels Oneota and Jacobs are moored.

In addition to its favorable location and configuration Stony Point Bay which earlier had been surveyed to establish depth contours and to determine the total area of the bay provided a basis for quantitative calculations of productivity in the periphyton community.

Routine sampling of the natural periphyton in Stony Point Bay began during the summer of 1966. The samples were taken at depths of 2.5, 5, 10, 20 and 35 feet along a course perpendicular to the shoreline; each sampling station was marked permanently with an anchored buoy. Divers and sampling equipment were transported on the Oneota from Knife River Harbor to Stony Point Bay, where the vessel was anchored at the thirty-five foot station. Divers employing SCUBA techniques obtained three rocks of four to six inch diameter from each of the six sampling depths.

Details of the collection technique and laboratory method for quantitation have been described earlier. In the pigment studies, aliquots from the combined periphyton slurry from the total surface area of three rocks were used as a basis for calculations.

For the analysis of periphyton pigments in samples taken during 1966, twenty-milliliter aliquots of suspension were removed from each sample. When the suspension appeared less turbid than usual, a forty-milliliter aliquot was used. These aliquots were processed according to modification of a pigment extraction method suggested by Creitz and Richards (1955) for the analysis of phytoplankton. The detailed procedure is as follows. Each portion of periphyton suspension was filtered through a glass fiber filter (Gelman, Type A), and the collected material was fixed by washing with fifteen milliliters of saturated magnesium carbonate solution. The purpose of this washing was to provide buffering and thus prevent the conversion of chlorophyll to phaeophytin. Each filter was ground in a tissue grinder along with five milliliters of ninety percent reagent-grade acetone to effect pigment extraction. The material was transferred to a graduated centrifuge tube and the volume was adjusted to ten milliliters with acetone. The suspension was then centrifuged in a stoppered tube for ten minutes to produce a clear supernatant solution from which a five-milliliter aliquot was pipetted into a cuvette. Total chlorophyll was first estimated on the basis of readings made with a Klett-Summerson colorimeter, using a No. 66 Klett-Summerson filter (640-700 millimicrons) and ninety percent acetone as the zero absorption standard. The following formula was used to calculate total chlorophyll concentrations:

$$\text{Chlorophyll } (\text{Mg/cm}^2) = \frac{(0.28)\ (\text{Klett units})\ (2)\ (\text{L. of sample})}{10^3\ (\text{L. of aliquot})\ (\text{cm}^2 \text{ surface area})}$$

Results are expressed in terms of milligrams of chlorophyll per 100 square centimeters of rock surface and as milligrams of chlorophyll per 100,000 organisms.

Each of the pigment solutions tested in the K-S colorimeter was then transferred to an absorption cell and its spectrum from 350 to 700 millimicrons was scanned and plotted with the Beckman DK-2A spectrophotometer, again using ninety percent acetone as the reference. The ratio of reference to sample absorbance (R/S) of a split-beam single light source is plotted by the instrument, thus removing any error accountable to unexpected power modulation. Sample temperature was held constant at 30°C. by means of a control device mounted on the instrument. Absorbance values at wavelengths of 480, 510, 630, 645, and 665 millimicrons were taken from the charted data and used for calculation of chlorophyll a, b and c concentrations, as well as for calculation of astacin and non-astacin carotenoids. The formulas developed by Richards and Thompson (1952), which were used in these calculations, are shown below.

$$\text{Chlorophyll } \underline{a}\ (\text{mg/L}) = 15.6D_{665} - 2.0D_{645} - 0.8D_{630};$$

$$\text{Chlorophyll } \underline{b}\ (\text{mg/L}) = 25.4D_{645} - 4.4D_{665} - 10.3D_{630};$$

$$\text{Chlorophyll } \underline{c}\ (\text{MSPU}) = 109D_{630} - 12.5D_{665} - 28.7D_{645};$$

where D is absorbance at a given wavelength.

$$D_{res},\ 510 = D_{510} - .0026C_a - .0035C_b - .0021C_c;$$

$$D_{res},\ 480 = D_{480} - .0019C_a - .0136C_b - .0054C_c;$$

where D_{res} is the residual absorbance at a given wavelength after subtraction of the absorbancies of the chlorophylls.

Astacin carotenoids (MSPU/L) = $2(4.45D_{res},\ 510 - D_{res},\ 480)$

Non-ast. carotenoids (MSPU/L) = $7.6\ (D_{res},\ 480 - 1.49D_{res},\ 510)$

Results are converted to milligrams (or MSPU) of pigment per 100 square centimeters of rock surface, and to milligrams (or MSPU) per 100,000 organisms at various sampling depths.

As used above MSPU refers to millispecified pigment unit. It represents a specific, but undetermined weight of the pigment which should be about one milligram, based on the weights and absorption coefficients of related compounds (Richards and Thompson, 1952).

A Gilson differential-volumetric respirometer was used to determine the gross photosynthetic rate of the periphyton. This instrument measures volume changes as a gas is absorbed or evolved under constant temperature and pressure, producing a digital reading directly in microliters. A special cover of black plastic sheeting was constructed for the respirometer so that the respiration rate of periphyton organisms could be determined in total darkness. The instrument was equipped with a bank of floodlights to facilitate photosynthesis measurements. Four-milliliter aliquots of the periphyton-water suspension were pipetted into acid-cleaned Warburg flasks together with 1.92 milliliters of carbonate-bicarbonate buffer solution (Warburg Number 11). This solution is composed of 0.1 molar sodium bicarbonate (95 percent) and 0.1 molar potassium carbonate (five percent). The buffer insures a constant pH (8.2), provides an adequate carbon dioxide source for photosynthesis, and incorporates carbon dioxide evolved during respiration into the carbonate-bicarbonate system. The reaction flasks were attached to individual manometers, each of which was connected to a common reference flask. A mixture of five per cent carbon dioxide in air was introduced into the gas spaces above the samples. The flasks were shaken in a 20°C. water bath while manometer readings were made during alternate ten minute light (1500 foot-candles) and dark periods. A ten-minute equilibration interval was allowed before each light or dark test.

During the light periods, both photosynthesis and respiration occur, and manometer readings reflect net photosynthesis (oxygen evolution less oxygen absorption, or "P+R"). In the dark, only respiration occurs. The manometer readings, therefore, indicate oxygen absorption, or "R". The assumption was made that oxygen absorption (respiration) in the dark is volumetrically equal to absorption in the light. Therefore, gross photosynthesis rate could be determined on the basis of the formula P (ten minutes) = $-[R - (P+R)]$ (from Umbreit, *et al.*, 1964). A correction factor involving barometric pressure and water vapor pressure was applied to yield microliters of dry gas at 760 millimeters of mercury. The results of three separate runs on each sample were averaged and expressed as microliters of oxygen produced per hour per 100 square centimeter of rock surface, and as microliters per hour per milligram of total chlorophyll.

Dry weights were determined by filtering four-milliliter portions of the periphyton suspensions through pre-weighed membrane filters; each filter, with its collected material, was dried for one hour in an oven at 103°C. and weighed again. Results are expressed as milligrams per square centimeter of rock surface.

Periphyton volume was estimated by settling the material from forty milliliters of suspension for three hours in a narrow graduated cylinder. Thus the recorded volumes included small and varying amounts of sand and clay. Results are reported in terms of milliliters of periphyton per square centimeter of rock surface.

To calculate pigment concentrations on the basis of a standard number of organisms, a twenty-five milliliter aliquot was transferred to a sample bottle along with twenty-five milliliters of ten percent formalin. One milliliter of this suspension was pipetted into a Sedgwick-Rafter counting cell and allowed to settle for ten minutes. A binocular compound microscope fitted with a Whipple disc was used to count ten random fields at a magnification of 200 diameters. The total numbers of organisms per square centimeter of rock surface was used for calculation of milligrams of pigment per 100,000 organisms.

Field studies were continued during the summer of 1967 (June 9 to September 15) with accelerated routine sampling of the naturally occurring periphyton of Stony Point Bay. Three rocks were taken twice each week from sampling stations at 2.5, 5, 10, 15, 20 and 35 foot depths. Water temperature and light intensity readings were also recorded during each sampling run. The temperature of water near the bottom at each sampling station was determined by a diver carrying a standardized laboratory thermometer. Light intensity at each depth was measured with a GM submersible photometer. In addition, daily incident radiation was continually recorded during the summer by a photometer situated on the roof of the laboratory.

A study of the rate of establishment of periphyton in Stony Point Bay was initiated in June, 1967. In order to present natural conditions for growth, rocks from the bay itself which were already supporting periphyton growth were chosen for use as a substrate in the regrowth experiment. This natural substrate was chosen to avoid the deviations in growth which may be expected with the use of an artificial substrate. Rocks four to six inches in diameter were obtained from shallow water in the bay and transported to the laboratory, and rinsed with tap water. The rocks were then autoclaved for twenty minutes at a pressure of fifteen pounds per square inch (250°F.). After sterilization, the rocks were replaced in Stony Point Bay at depths of 10, 20, and 35 feet by SCUBA divers. The rocks were lowered in a wire basket to the divers, who placed them on the bottom in a circle around the anchor of a marker buoy. After predetermined "incubation" periods, ranging from eight hours to 101 days, three rocks were retrieved from each depth by divers employing the plastic bag technique.

In addition to the regular sampling of Stony Point Bay, an investigation of the periphyton of other north shore areas was carried out during the summer of 1967. Eleven stations approximately ten miles apart along a 107 mile segment of the north shore of Lake Superior were selected for sampling of the periphyton community. These stations ranged from the southernmost at Lester River to the northernmost at Grand Marais, Minnesota. Three rocks were taken from depths of 2.5, 5, 10, 15, 20 and 35 feet except in certain cases where no rocks were encountered at the 35 foot depth.

Samples collected from Stony Point Bay and the other north shore stations during the summer of 1967 were prepared for laboratory examination by the same basic procedures as described previously. Pigment analyses were performed on all samples in the same manner as in 1966, except that the K-S colorimeter was not used to estimate total chlorophyll. Photosynthetic rate under standard conditions was again determined for each sample from Stony Point Bay. Since the addition of carbon dioxide to the reaction flasks seemed to pressurize the system and produce high results, none was added during the 1967 measurements. Due to the large number of samples collected in a short period of time from the other north shore stations, photosynthetic rates of only a limited number of these samples could be determined.

In addition to the determination of total dry weights, the samples were analyzed for ash-free (organic) dry weight. A twenty-five milliliter aliquot of each periphyton suspension was drawn through a preweighed four-centimeter filter paper. The filters were placed in preweighed porcelain crucibles and dried for one hour in an oven at 103°C. After the crucibles had been cooled in a desiccator and reweighed, they were placed in a muffle furnace at 600°C. for fifteen minutes. After cooling in the desiccator, the ashed samples were weighed again for the calculation of ash-free dry weights. Results are expressed as milligrams of total dry weight and ash-free dry weight per square centimeter of rock surface.

The second phase of the investigation began in June, 1968. It was designed to provide information regarding the effects of short-term changes in light intensity and temperature on the productivity of Lake Superior periphyton. The general procedure was to "condition" or acclimate, natural periphyton samples to various light intensities and temperatures for short periods in the laboratory and then to determine the photosynthetic rates of the conditioned samples in crossed gradients of light intensity and temperature. Analysis of photosynthetic pigment concentrations in conditioned samples provided a basis for the calculation of assimilation values for periphyton organisms under a variety of conditions. The rate of change of pigment concentrations following an increase or reduction of light intensity was also examined.

To facilitate the conditioning of periphyton organisms in a simulated lentic situation, special incubators were designed for use in the laboratory. Each of four Precision B.O.D. incubators with variable temperature control was modified to enclose a ten-liter plastic tub which served as a sample container. Two banks of fluorescent lamps (General Electric daylight white, 20 inch) were mounted in a vertical position along the inside walls of the incubators. The light intensity within the incubators could be altered by adding, removing or masking lamps in the lighting system. A Weston light meter reading directly in foot-candles was used to measure light intensity in the incubators. A continual-flow water circulation system was installed in each incubator for the purpose of maintaining a steady, slow flow of water through the sample container. A variable-speed peristaltic pump mounted on the top of the incubator circulated water through the sample container by means of 3/8-inch Tygon tubing. The inlet and outlet tubing reached from the pump to the sample container through two small holes drilled in the side of the incubator. The inlet tube reached slightly below the surface of the water in the container, while the outlet tube was anchored to the bottom in the opposite corner of the container. A four-liter plastic aspirator bottle was suspended above the sample container inside the incubator and tied into the inlet line. This bottle could be disconnected and removed at selected intervals and replaced with another bottle full of fresh water, thus serving as a means for maintaining a rather constant level of nutrients in contact with the samples.

Rocks with well established growths of periphyton were carefully collected by hand from Stony Point Bay and placed in buckets of water for transport to the laboratory. The rocks were transferred to the sample containers in the incubators. Water from Stony Point Bay was collected daily in a large carboy and used as the medium for sustaining growth of the samples in the containers; the rocks were submerged in seven liters of water. To simulate the lentic situation, the pumps were arbitrarily set to recirculate the water at a rate of 350 milliliters per minute. This rate allowed a retention time of twenty minutes in the sample container. During all experiments, the medium was partially changed each day by replacement of the aspirator bottle. Water pumps and individual ballasts for each fluorescent lamp were located outside the incubators to disperse the heat developed during operation.

Four different sets of conditions for incubation could be provided at one time by selecting various combinations of temperature and light intensity within the incubators. After a specified time period, the rocks were usually removed from the incubators and the attached periphyton removed for analysis as previously described. Pigment analyses and ash-free dry weight determinations were performed as in the field study. Organisms were microscopically examined, counted and identified to species if possible. For the determination of photosynthetic rates under different conditions, it was necessary to alter the respirometer so that various light intensities could be produced. This was accomplished by removing certain lights from the apparatus and positioning the flasks in such a way as to provide different light intensities at nine flask locations (20, 60, 80, 180, 300, 400, 600, 900 and 1500 foot-candles). These intensities were determined with the Weston light meter. Photosynthetic rates of conditioned samples were measured at the nine light intensities and at a variety of temperatures by employing the automatic water bath temperature control on the respirometer. Several experiments were run each designed to examine a separate problem and each employing the general procedures just described.

In 1969 and 1970 the study was expanded to include observations on periphyton growth in Lake Superior water which had been pumped into holding pools where certain environmental controls could be imposed to modify the normal lake water while adequate controls were being maintained. This also presented an opportunity for a study of the contributions periphyton might make to the lake plankton.

To provide an aquatic environment for periphyton growth which would be both natural and yet capable of experimental modification, a field station consisting essentially of two rock-basin pools, a piping system and a small building to house the pumping, metering and other necessary equipment was established on a relatively isolated stretch of shoreline near Castle Danger, Minnesota. This particular section of shoreline comprises part of a 50-acre tract of lakeshore property owned by the University of Minnesota (UMD) and is located about 40 miles from the base laboratory (Lake Superior Limnological Research Station) at the Lester River in Duluth.

In order to determine the best site for pool construction, a preliminary survey was made covering approximately one-third mile of shoreline within this area. A specific site was eventually found which met all of the predetermined criteria used in the survey: (1) The rock stratum was to be sufficiently level and large enough to assure exposure of both pools to sunlight of equal intensity; (2) The elevation above lake level had to be high enough to prevent ordinary or moderately-sized waves from splashing excessive water into the pools; (3) The bank above the pools should have a slope which would minimize the possibility of seepage and surface runoff; (4) The area should be fairly well protected from the effects of periodic storms; (5) The rock substrate, itself, had to be solid and not excessively "granular" or full of fissures; and lastly, (6) The pools had to be near a source of electricity to provide power for the pumps.

Construction of the pools began in the middle of July, 1969. Using air-hammers, two basins were excavated in the solid gabro rock bed, one with an approximate capacity of 3,000 gallons and the other with a slightly smaller capacity of 2,500 gallons (Figs. 1, 2). The entire bottom and as much as possible of the side surfaces were formed of the natural rock. Concrete blocks reinforced with iron rods were used only where necessary to fill in irregularities and to form the rims of the pools. To minimize leaching of calcium from the cement blocks, the walls were scrubbed with a solution of technical grade hydrochloric acid and, as a final chore, any cracks or fissures present were patched with an inert hydraulic cement sealer known commercially as "Thoroseal".

The exact capacity of each pool, when filled with water to a level about two inches below the rim, was calculated by measuring the flow rate of the incoming water and the time required to fill the pools. For this preliminary determination, flow meters were temporarily installed on each branch of the single intake pipe. The pool with the larger capacity, designated as the "control pool", contained 394 cubic feet (2,950 gallons) of water; the "test pool" was of slightly smaller capacity and contained 337 cubic feet (2, 520 gallons) of water. The water level in both pools was regulated and maintained at the previously mentioned height by means of 2" overflow pipes on the outside of the front walls.

As shown in Plate 1, the control pool was built at a slightly higher elevation than the test pool. This higher level coupled with a greater volume was intentionally designed to eliminate or, at least, substantially reduce any diffusion which might occur between the two pools through their common center wall. If diffusion were to occur it would, therefore, be directed from the control pool to the test pool due to the greater water pressure in the former. This is an important consideration since the water in the test pool was experimentally enriched and any diffusion in the reverse direction would alter the natural quality of the lakewater in the larger pool and, thus, invalidate its use as a control.

Using a ½-hp pump, lakewater was drawn into a single T-shaped intake pipe and continually cycled through both pools, resulting in an average of six overturns per day. An "American series" flow meter installed on each arm of the inlet line indicated that the flow through the control and test pools was approximately 18,000 gallons/day and 15,000 gallons/day, respectively.

Solutions containing 0.163 ppm phosphate as PO_4-P and 1.96 ppm nitrate as NO_3-N were added to the test pool with a ¼-hp American Meters Co. Proportioning pump. Any change in concentration of these ions was monitored by chemical analysis of water samples collected daily from both pools. Phosphate concentration was measured by the stannous chloride method (APHA Standard Methods, 1965) and nitrate nitrogen was determined by both the phenoldisulfonic acid method (APHA Standard Methods, 1965) and an Orion Ion-Analyzer equipped with a nitrogen-specific electrode. Since the amounts of phosphorus and nitrogen added to the test pool were always maintained in a 1:15 ratio, the concentration of phosphate could also be calculated from the nitrate analyses.

In 1969, periphyton-covered rocks lying 2-3 feet below the surface were initially collected from a relatively sheltered area along the shore. However, it was subsequently found that many of these rocks were extremely jagged and irregular in outline and therefore would not be suitable to the study because of the uncertainty involved in determining the surface area and the difficulty of completely removing the natural growth as would be later required. For this reason, another survey was begun along the entire shoreline within the boundaries of the University-owned property to find an area in which the rocks would be more uniform in shape, size and degree of periphyton growth. The use of SCUBA gear allowed underwater exploration at considerable distances outward from the shore and, thus, a much greater area of the lake bottom was able to be examined at depths ranging from three to twenty feet.

Rocks of adequate size were frequently noted at depths of 5-9 feet but their surface was usually covered with patches of green filamentous forms and rather uneven periphyton distribution. A suitable area was finally located at a depth of 12 feet in a small bay about

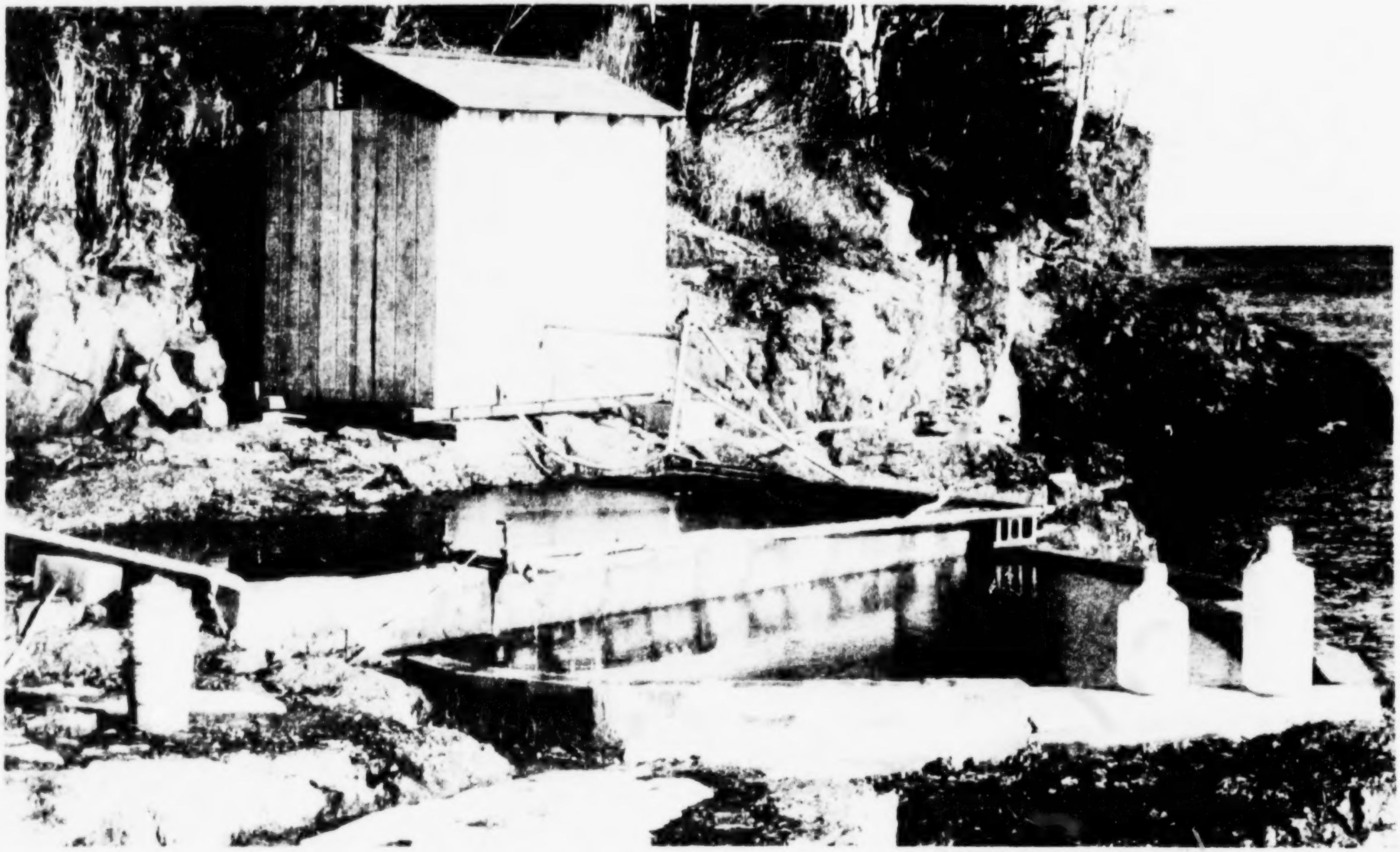

Plate 1. Experimental pools for periphyton studies on North Shore of Lake Superior at Castle Danger, Minnesota. Note the lower level of the test pool in the foreground.

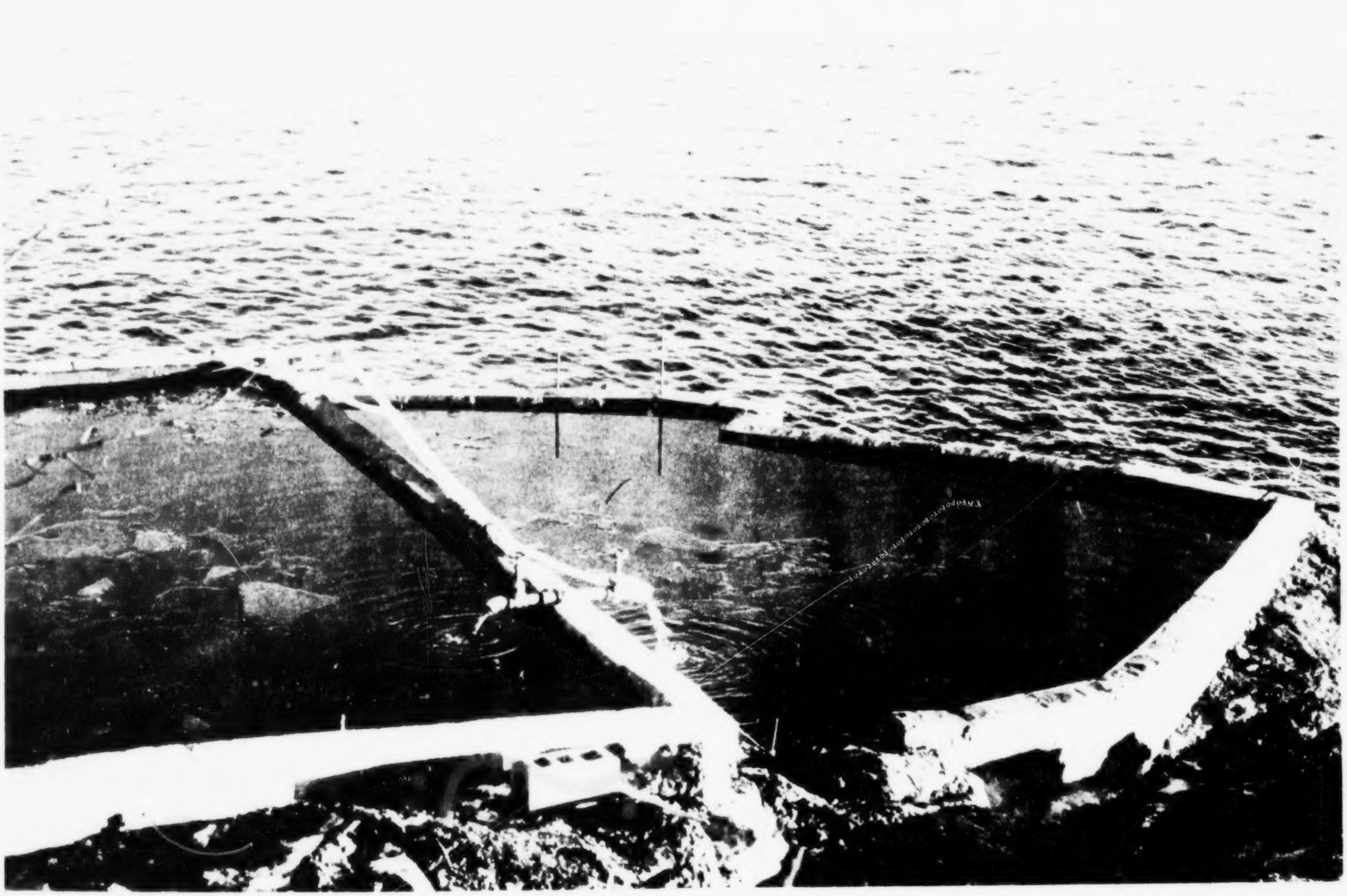

Plate 2. Experimental pools for periphyton studies on the North Shore of Lake Superior, Castle Danger, Minnesota, showing piping arrangement to control pool (left) and test pool (right).

one-quarter mile from the field station. In contrast to the patchiness observed previously, the periphyton at this depth appeared to be more uniform and the rocks were heavily coated with the wooly brown growth characteristic of diatoms.

Rocks from this site were collected by the underwater method described for Stony Point Bay. Within a period of two hours, a total of 120 rocks, similar in shape and approximately 7-9 inches in diamter, were selected and repositioned in the experimental pools. At the field station, the plastic bags were carefully removed and 60 rocks were aligned in north-south rows in each of the half-filled pools. The rocks in each pool were individually placed in a position similar to their original orientation on the lake bottom and at a sufficient distance from the walls to prevent unequal shading and, consequently, any discrepancies which could be attributable to differences in length of exposure to sunlight. The pools were then filled with lakewater and, after a one-week period of stabilization, phosphorus and nitrogen were added to the test pool.

At weekly intervals thereafter two sample rocks were removed from each pool and placed in individual plastic bags. The rocks were gathered either by using hip waders and stepping directly into the pools to remove the specimens or by temporarily spanning the pools with a 16-foot board from which, by lying face downward, it was possible to retrieve the rocks from any desired depth or location. Following the method of Fox and Stokes, as cited previously, the samples were randomly collected from various areas of both pools with as little as possible discrimination regarding visible growth. Collections were usually made in the late morning and the samples were promptly returned to the base laboratory where they were processed no later than four hours afterwards.

Biological and chemical analyses were done in the laboratory at the Lake Superior Limnological Research Station in Duluth. Procedures for periphyton recovery and delineation of rock surface area were the same as those which have been described previously.

A microscopic examination was made of both the periphyton and the phytoplankton in the experimental pools. After the growth outline had been scratched onto the rock surface, the periphyton were scraped off with a stiff plastic brush and, together with a small amount of distilled water used in rinsing the rock and the plastic bag, the total fluid suspension was measured in a graduated cylinder and transferred to a small plastic pail from which the samples for identification and enumeration were obtained.

Although a large, inverted funnel was immersed and rapidly agitated in the liquid periphyton suspension, the mixture remained fairly thick and dilutions ranging from 2:1 to 8:1 were made prior to examination. Due to the abundance of filamentous algae in the sample a cut-off 10-ml pipette, instead of the 1-ml pipette normally employed, was used to transfer a one-milliliter aliquot to the Sedgewick-Rafter counting cell. Organisms were examined with a binocular microscope at 200X magnification and ten random fields were counted.

For phytoplankton examination, 4-liter water samples were collected twice a week from (a) the lakewater intake pipe, (b) control pool effluent pipe, and (c) test pool effluent pipe. The samples were qualitatively and quantitatively examined using the drop method developed by Lackey during his investigations of the Scioto River, Ohio (APHA Standard Methods, 1965). In this method, most of the supernatant liquid from the centrifuged sample is removed and the concentrate is re-suspended in the small amount of fluid remaining. After having established the ratio between the number of drops in the concentrate and the volume of the original sample, one drop is transferred to a glass slide and a coverslip is immediately applied. In this study, the organisms were counted in four microscopic traverses using a medium-power 20X objective (4 strips at this magnification (200X) being considered equivalent to 8 strips at 44X or 2 strips at 100X).

The temperature of the water in both pools and that of the lakewater from the intake pipe was monitored daily with an electronic thermometer coupled to a recording chart unit. General environmental conditions which could possibly influence the nature of the results, such as storms or high winds, were also noted and recorded. Since, for Lake Superior, lists of periphyton species are not available, a special study was undertaken during the summer of 1970 to provide such a reference. This list is based on the Castle Danger Studies and the accumulated observations (1965-1970) on the near-shore periphyton along the North Shore. Dr. Alan J. Brook, R. Colingsworth and other experts were consulted. On the basis of their assistance and the personal judgement of the senior investigators a species list has been prepared.

SECTION V

RESULTS OF PERIPHYTON DISTRIBUTION AND TAXONOMY STUDY

For the sake of simplicity findings are reported here in chronological order, and to avoid unnecessary repetitions, the results and the discussion of results have been combined. In this section therefore, one will find the presentation and summation of data obtained over the entire four year period of study, namely, 1965, 1966, 1967, and 1968.

Stony Point Bay was the primary sampling area. Its location and a detailed presentation of the sampling area are shown in Figures 1 and 2. As may be seen from Figure 2, the study area is triangular, bounded by Rocky Point on the northeast, the Little Sucker River on the southwest, and a reference buoy in the lake 2,236 feet from shore. The total area enclosed by these three points is approximately 321,000 square meters. The straight line distance from Rocky Point to the Little Sucker River is about one half mile.

Initial observations made of the bay showed that the surrounding land area was very sparsely populated. The only spectators noticed during the course of our operations were an occasional tourist or commercial fisherman. Permanent cribs for holding fish were noted in the bay. One fisherman complained of the slimy growth which often fouled his nets and pointed out periphyton on some nearby rocks as the cause. Earlier unpublished studies made by one of the authors (Olson, 1960) support the hypothesis of the fisherman. In microscopic examinations of the growths on fish nets from other areas of Lake Superior, Olson found diatoms attached by gelatinous stalks. The organisms were primarily members of the genus Cymbella.

The water of Stony Point Bay appeared either blue, green, gray, tan, or intermediate shades, depending on the cloud cover, the nature of the bottom, and the turbidity produced by living or non-living suspended materials. Secchi disc readings likewise varied, with the maximum being about eight meters. The bottom type could usually be determined visually in depths of up to twenty feet. Maximum visibility in the bay, as reported by SCUBA divers, was about thirty feet. In general, water temperatures in the early summer were about 6°C. just under the surface and 4.5°C. at thirty-five feet.

In preparing a report on the nutrients of the western arm of Lake Superior, Putnam and Olson (1960) obtained their data from a large number of samples collected from the Larsmont-Knife River area, which is approximately two miles from Stony Point Bay. The mean values that they obtained for several chemical parameters (from July 15 - September 10, 1959 are as follows:

	Epilimnion	Hypolimnion
Silica (ppm)	2.04	2.13
Carbon dioxide (ppm)	1.28	2.33
Nitrate (ppm)	0.36	0.42
Organic nitrogen (ppm)	0.14	0.13
pH	7.9	7.7
Phosphorus, total (ppm)	0.01023	0.0136
Oxygen saturation (%)	105	97
Alkalinity (ppm)	38.5	

Routine analyses performed during each of the summers, 1964 to 1968, by School of Public Health students show that these values have remained essentially the same. In fact, when even slight variations from these values were obtained, the deviation could almost invariably be traced back to faulty laboratory technique.

In 1960, the predominant genera of phytoplankton taken in the Larsmon-Knife River area were Asterionella, Cyclotella, Fragilaria, Melosira, Synedra, Tabellaria, Dinobryon, and Ankistrodesmus (Putnam and Olson, 1961). Counts made in 1968 showed that the same organisms were predominant and that in August, Dinobryon sertularia was the most common organism in the phytoplankton.

Periphyton was visible generally throughout the Stony Point Bay area, on the rocks appearing as a thick, tan, wooly growth containing entrapped gas bubbles (presumably oxygen) causing them to rise to the surface. It was observed that wave action occurring as a result of a storm would dislodge the periphyton from the rocks in the shallow areas of the bay. The resulting suspension imparted a distinct tan color to the water and sometimes reduced visibility to zero. Sculpins (genus Cottus), ranging in size from one to four inches, were the only fish observed. Occasionally, Mysis relicta, a species of minute crustacean was seen swimming in groups of ten to twenty individuals near the bottom. On one occasion, several clumps of an attached, filamentous, macroscopic green alga, Nitella, were observed.

In general, the bay floor was uniformly covered with a tan mat of periphyton, on both the sand and the rocks. The rocks on which the growth occurred ranged in size from less than an inch in diameter to boulders projecting as much as six feet above the bottom. Animal forms sometimes seen in this periphyton were leeches, snails, nematodes, caddisfly larvae, and mayfly nymphs.

When the rocks were scrubbed clean in the laboratory, it was noted that they differed markedly in appearance. An analysis of one hundred representative rocks indicated that there were about twenty -two lithic types in Stony Point Bay (see Table I). The majority (fifty-six per cent) of the rocks were basalt, with twenty-four per cent of these possibly being wither andesite (sixteen per cent) or diabase (eight per cent). The next most common rock type was diabase, with fourteen positive identifications. Seven per cent of the rocks were porphyritic trachyandesite to mafic quartz latite.

The 1965 regrowth study, in which denuded, autoclaved rocks were replaced in the lake, provided the first qualitative periphyton data. Nineteen different rocks were recovered from depths of from two to nineteen feet. "Incubation" times ranged from three to twenty-seven days. Thirty-four different genera from three phyla of algae were found in the regrowth on these rocks, they are listed in Table II. Although not shown in the table, some genera were represented by more than one species. Of the thirty-four genera, twenty-five, or seventy-four per cent, were members of the phylum Chrysophyta and twenty-four of these were diatoms. The one remaining genus, Dinobryon, belongs to the class Chrysophyceae. Next in order of abundance was the phylum Chlorophyta. Seven genera of these green algae were found. Blue-green algae were represented by only two genera.

TABLE I

ROCK IDENTIFICATIONS, STONY POINT BAY, LAKE SUPERIOR.

Number of Samples	Lithic Description
2	medium to coarse grained granite
1	porphyritic andesite
1	massive graywacke
1	laminated hornfels, pelitic
2	fine grained, porphyritic, red granophyre
10	aphanitic to fine grained basalt, aphyric
2	very fine grained basalt with small amygdules
16	very fine grained porphyritic basalt or andesite
7	very fine grained porphyritic trachyandesite to mafic quartz latite (intermediate)
2	fine grained porphyritic trachyandesite
1	very fine grained porphyritic felsite
6	fine to medium grained amygdaloidal basalt
11	aphanitic to very fine grained ophitic basalt
3	fine grained ophitic basalt
8	fine to medium grained basalt or diabase
6	fine grained diabase
14	fine to medium grained diabase
2	anorthositic gabbro
1	anorthositic olivine gabbro
1	porphyritic gabbroic anorthosite
2	arkosic sandstone (one red, one white)
1	red siltstone
100 = Total	

Although in 1965 the study was limited to qualitative observations, it was observed that the number of genera increased with increased "incubation" time. In the shallow area, only *Cymbella*, *Diatoma*, *Gomphonema*, *Melosira*, and *Synedra* occurred. These same groups plus thirteen additional genera were observed in the sample from deeper water. Several factors may be responsible for this phenomenon. Wave action in the shallower water may make the attachment process difficult for some genera. Certain genera may be more capable of withstanding rough water. Also, waves undoubtedly knock periphyton from the rocks into the water, thereby reducing both numbers and kinds of organisms. Finally, selective grazing by insects and other organisms may also be a contributing factor in preventing the establishment of certain genera on rocks in shallow water.

The results of Douglas (1958) support the latter hypothesis. She found a negative correlation between populations of *Achnanthes* and the caddisfly larvae, *Agapetus fuscipes*, in studying the periphyton of an English stream. She stated that her findings suggest a grazing effect. In Stony Point Bay, *Achnanthes* is a common diatom and caddisfly larvae occur, especially in shallow water. Douglas also noted shifts in the populations of *Gomphonema* and *Synedra* which could be attributed to grazing. It is interesting to note that these forms are also common in Stony Point Bay.

It was not felt that the varying rock types affected the growth of the periphyton in any way, inasmuch as two different types of rock from the same depth "incubated" for a like amount of time seemed to support similar numbers of the same genera of organisms. Although no specific experiments were conducted to verify this observation, later quantitative findings supported the hypothesis.

In 1965, another pertinent find was that a growth made up of eighteen genera of algae could be produced on rocks "incubated" for only three days in the lake. This information suggested that initial colonization of a denuded, autoclaved rock could take place in a very short time and provided the basis for planning future studies, in which rocks were examined as early as eight hours after being replaced in the lake.

Although quantitation was not the objective of this preliminary study, a purely subjective estimation of abundance indicated that *Achnanthes* and *Synedra* were predominant in the majority of samples.

In addition to the microscopic examination, dry weight determinations were also made on the periphyton of Stony Point Bay. Samples came from depths of two, ten, and twenty feet and weights were expressed as milligrams per square centimeter of rock surface. The results are presented in Table III. Each depth was sampled on seven different days in July and August. It will be noted that the weights are quite variable and that no seasonal trends are apparent. In terms of mean weights for the seven days, the ten foot samples were the highest, the

TABLE II

A CHECKLIST OF LAKE SUPERIOR PERIPHYTON OCCURRING AS REGROWTH ON ARTIFICIALLY DENUDED ROCKS, STONY POINT BAY, LAKE SUPERIOR, 1965.

Phylum Chrysophyta

- Class Bacillariophyceae
  - *Achnanthes microcephala* (Kuetzing) Cleve
  - *Amphora ovalis* Kuetzing
  - *Amphora normani* Rabenhorst
  - *Asterionella formosa* Hassall
  - *Ceratoneis arcus* (Ehrenberg) Kuetzing
  - *Cocconeis flexella* (Kuetzing) Cleve
  - *Cocconeis* spp.
  - *Cyclotella* spp.
  - *Cymatopleura solea* (Brebisson) W. Smith
  - *Cymbella lanceolata* (Ehrenberg) Van Heurck
  - *Cymbella* spp.
  - *Denticula thermalis* Kuetzing
  - *Diatoma elongatum* C.A. Agardh var. *tenuis* (Agardh) Van Heurck
  - *Diploneis elliptica* (Kuetzing) Cleve
  - *Fragilaria capucina* Desmazieres
  - *Fragilaria crotonesis* Kitton
  - *Gomphonema geminatum* (Lyngbye) C.A. Agardh
  - *Gomphonema* spp.
  - *Melosira granulata* (Ehrenberg) Ralfs
  - *Melosira* sp.
  - *Navicula* spp.
  - *Nitzschia* spp.
  - *Pinnularia* sp.
  - *Rhizosolenia eriensis* H.L. Smith
  - *Rhoicosphenia curvata* (Kuetzing) Grunow
  - *Surirella* spp.
  - *Stauroneis* spp.
  - *Stephanodiscus* sp.
  - *Synedra acus* Kuetzing
  - *Synedra rumpens* Kuetzing
  - *Synedra ulna* (Nitzsch) Ehrenberg
  - *Tabellaria fenestrata* (Lyngbye) Kuetzing
  - *Tabellaria flocculosa* (Roth) Kuetzing
- Class Chrysophyceae
  - *Dinobryon sertularia* Ehrenberg

Phylum Chlorophyta

- *Actinastrum* sp.
- *Cosmarium* sp.
- *Closterium* sp.
- *Coelastrum* sp.
- *Oedogonium* sp.
- *Scenedesmus quadricauda* (Turpin) Brebisson
- *Tetraedron minimum* (A. Brown) Hansgirg

Phylum Cyanophyta

- *Anacystis* sp.
- *Merismopedia convoluta* Brebisson

twenty foot samples the lowest, and the two foot samples were intermediate. Although the variation between these three means is relatively small, the figures reported are logical. For instance, it is possible that the two foot mean is lower than that for ten feet because of the fact that wave action dislodges more periphyton at the shallower depth. The lower weight at twenty feet may be explained by the fact that in deeper water there is less light penetration and therefore fewer photosynthetic organisms. Also, lower temperatures exist in deeper water and could be expected to retard growth rate.

On the basis of the mean dry weight figure for the three depths (July 27 to August 23) and the area of the bay, a rough estimate of the average total dry weight, or the standing crop, of the periphyton on the floor of Stony Point Bay was 54.4 tons (153 g/m^2).

TABLE III

NATURALLY OCCURRING PERIPHYTON DRY WEIGHTS AT SEVERAL DEPTHS, STONY POINT BAY, LAKE SUPERIOR, 1965. MILLIGRAMS PER SQUARE CENTIMETER OF ROCK SURFACE.

	Depth in feet		
Date	2	10	20
7-27	12.8	28.5	25.5
8-3	39.2	18.1	6.4
8-9	3.1	10.1	3.5
8-12	8.4	8.0	8.4
8-16	17.2	14.4	20.1
8-19	20.2	36.8	19.1
8-23	5.1	5.0	13.3
Mean	15.1	17.3	13.8

The marked reductions in dry weights that occurred on August 9 and 23 (Table III) are compatible with the theory that a counterclockwise current is produced within Stony Point Bay during the time of a strong northeast wind. An east wind would have the same effect, only to a lesser degree. The current thus produced could then loosen and dissipate the periphyton, thereby reducing its volume. The depth at which the periphyton could be affected would depend on the velocity of the current. U.S. Department of Commerce climatological data, obtained from the Duluth International Airport, strongly support this hypothesis. During August of 1965, northeast winds were recorded for only three days. They occurred on August 7, 8, and 23. These dates all correspond with those on which the low weights were obtained.

In 1966, samples were examined quantitatively as well as qualitatively. From August 9 to September 6, twenty-seven samples of three rocks each were obtained from Stony Point Bay at depths of 2.5, 5, 10, 15, 20 and 35 feet. The results are presented in Figure 3 and Tables IV to VI.

The numbers of naturally occurring periphyton organisms found per square centimeter of rock surface, plotted against the six standard sampling depths, are shown in Figure 3. Numbers are means of the totals found at each depth for the five sampling days. The mean at the 2.5 foot depth was 490,000 per square centimeter, which was lower than the five foot mean of 587,000 per square centimeter. This was possibly due to the dislodgement of the organisms by wave action. The ten foot mean of 433,000 per square centimeter and the fifteen foot mean of 365,000 per square centimeter showed that there was a downward trend. This could be explained on the basis of lower temperatures and less light penetration in the deeper water. Because of these two factors, the twenty foot mean of 468,000 per square centimeter and the thirty-five foot mean of 637,000 per square centimeter were unexpectedly high. The only plausible explanation is that the unusually rough weather which occurred during the summer of 1966 dislodged the periphyton up to depths of at least twenty feet, and possibly affected growth beyond that point to a lesser degree. In discussing these counts, the numbers have been rounded off to the nearest thousand. A mean of the counts at all depths is 497,000 organisms per square centimeter of rock surface.

A list of the genera observed while making the counts is presented in Table IV. Of the twenty-four genera listed, nineteen, or seventy-nine percent, are members of the phylum Chrysophyta. Only one of these, Dinobryon, is not a diatom. Four genera of green algae (Chlorophyta) were observed. The phylum Cyanophyta was represented by only one blue-green alga, Merismopedia.

It would be logical to expect more genera of organisms to be present in the naturally occurring periphyton sampled during 1966 than in the 1965 regrowth periphyton. This was not the case. In 1965, thirty-four genera were found occurring as regrowth, while only twenty-four genera were observed in the naturally occurring periphyton of 1966. This difference in the number of genera is probably a result of the differing procedures used in examining the two sets of samples. In 1965, periphyton was examined qualitatively, with the desired result being identification to species. For this reason, a good deal of time was spent on each sample and many organisms were examined. In 1966, the goal was to identify the organisms to genus and quantitate them. A ten random field counting method was used. By using this method, fewer organisms were encountered than during the 1965 examinations. In addition, the total number of samples examined during 1966 was relatively small. All but one of the genera, Ankistrodesmus, observed in the naturally occurring periphyton in 1966 had been found in the 1965 regrowth samples. Genera of organisms encountered during 1965 and not reported for 1966 include: Chrysophyta - *Ceratoneis*, *Diploneis*, *Pinnularia*, *Rhoicosphenia*, *Stauroneis*, and *Stephanodiscus*; Chlorophyta - *Actinastrum*, *Cosmarium*, *Coelastrum*, and *Oedogonium*; Cyanophyta - *Anacystis*.

The numbers of organisms from each of the three phyla which characterize the periphyton of Stony Point Bay and the total counts of each sample are presented in Table V. It can be seen that diatoms were found in all of the twenty-seven samples, while one or more of the genera of Chlorophyta were found in eleven samples. *Merismopedia*, the only blue-green, was observed in ten samples. *Dinobryon*, the only member of the phylum Chrysophyta that is not a diatom, was found in low numbers in thirteen of the samples. This organism, therefore, can be considered an insignificant contributor to the total numbers of Chrysophytes. The distribution of phyla according to depth is interesting, although possibly not significant. All three phyla were observed at 2.5, 5, 10, and 20 feet. At fifteen feet, however, no greens or blue-greens were found. At thirty-five feet, no greens were observed. Because of the narrow time span over which the sampling occurred and the rough weather, it would be unrealistic to intimate that these organisms were responding to seasonal changes.

In Table VI, seven genera, all diatoms, are listed in the order of abundance. This listing has been done on the basis of the average of the means of the percentage compositions of each organism at all six depths. These results confirm the earlier judgement that *Achnanthes* and *Synedra* were the most common organisms. The average of the mean percentages for all depths of *Achnanthes* is 32.1 per cent, while a comparable figure for *Synedra* is 26.4 per cent. At every depth on all sampling days, these two organisms together comprised greater than fifty per cent of the total count.

TABLE IV

GENERA OF ORGANISMS OBSERVED IN NATURALLY OCCURRING PERIPHYTON, STONY POINT BAY, LAKE SUPERIOR, 1966.

- Phylum Chrysophyta
  - Class Bacillariophyceae
    - *Achnanthes*
    - *Amphora*
    - *Asterionella*
    - *Cocconeis*
    - *Cyclotella*
    - *Cymatopleura*
    - *Cymbella*
    - *Diatoma-Denticula*
    - *Fragilaria*
    - *Gomphonema*
    - *Melosira*
    - *Navicula*
    - *Nitzschia*
    - *Rhizosolenia*
    - *Surirella*
    - *Synedra*
    - *Tabellaria*
    - Unidentified
  - Class Chrysophyceae
    - *Dinobryon*
- Phylum Chlorophyta
    - *Ankistrodesmus*
    - *Closterium*

TABLE IV (Continued)

Phylum Chlorophyta (Continued)

  Scenedesmus
  Tetraedron

Phylum Cyanophyta

  Merismopedia

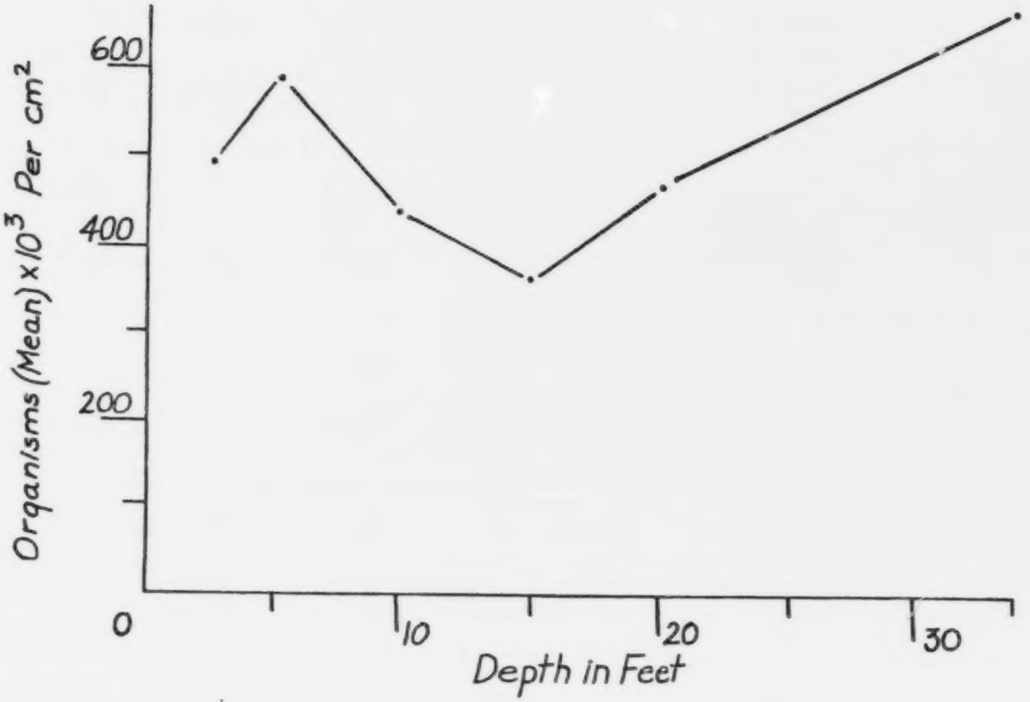

Figure 4. Mean total counts of naturally occurring periphyton at the standard sampling depths, Stony Point Bay, Lake Superior, 1966.

TABLE V

PHYLA AND COUNTS OF ORGANISMS OBSERVED IN NATURALLY OCCURRING PERIPHYTON, STONY POINT BAY, LAKE SUPERIOR, 1966. ORGANISMS x 10^3 PER SQUARE CENTIMETER OF ROCK SURFACE.

Depth in Feet	Phylum	Date 8-9	 8-17	 8-23	 8-25	 9-6
2.5	Chrysophyta	N.S.*	319.9	417.5	562.3	641.2
	Chlorophyta		4.6	---	---	3.4
	Cyanophyta		2.3	---	---	6.7
	Total		326.8	417.5	562.3	651.3
5	Chrysophyta	N.S.	710.1	592.3	551.0	470.8
	Chlorophyta		5.2	2.6	---	9.0
	Cyanophyta		2.6	---	---	---
	Total		717.9	597.5	551.0	479.8
10	Chrysophyta	568.1	271.8	523.5	419.6	360.4
	Chlorophyta	5.0	1.8	2.8	3.2	---
	Cyanophyta	5.0	---	---	---	3.4
	Total	578.1	273.6	526.3	422.8	363.8
15	Chrysophyta	703.9	172.7	N.S.	193.9	389.7
	Chlorophyta	---	---		---	---
	Cyanophyta	---	---		---	---
	Total	703.9	172.7		193.9	389.7
20	Chrysophyta	699.6	355.3	321.8	504.4	446.0
	Chlorophyta	---	2.8	5.4	---	---
	Cyanophyta	---	---	---	2.6	---
	Total	699.6	358.1	327.2	507.0	446.0
35	Chrysophyta	778.7	759.6	491.9	525.4	623.1
	Chlorophyta	---	---	---	---	---
	Cyanophyta	3.0	---	---	2.6	1.9
	Total	781.7	759.6	491.9	528.0	625.0

*N.S. means no sample was collected because of rough weather. Three dashes mean zero.

TABLE VI

COUNTS AND PERCENTAGE CONTRIBUTION TO THE TOTAL OF THE SEVEN MOST COMMON ORGANISMS OBSERVED IN THE NATURALLY OCCURRING PERIPHYTON, STONY POINT BAY, LAKE SUPERIOR, 1966. ORGANISMS x 10^3 PER SQUARE CENTIMETER OF ROCK SURFACE AND PERCENTAGE.

Organism	Depth in Feet	8-9	8-17	8-23	8-25	9-6	Mean
Achnanthes	2.5	N.S.*	128.9	133.0	121.5	175.5	139.7
		N.S.	42.8%	31.9%	21.6%	26.9%	30.8%
	5	N.S.	356.5	248.7	224.9	172.1	250.5
		N.S.	49.7%	41.6%	40.7%	35.9%	42.0%
	10	259.1	60.4	124.3	123.0	115.6	136.4
		44.8%	22.1%	23.6%	29.1%	31.8%	30.3%
	15	274.1	52.7	N.S.	40.9	133.1	125.2
		38.9%	30.9%	N.S.	21.1%	34.2%	31.2%
	20	148.3	147.3	119.1	113.0	108.5	127.2
		21.2%	41.1%	36.4%	22.3%	24.3%	29.1%
	35	323.4	238.9	122.9	147.9	129.1	192.4
		41.4%	31.5%	25.0%	28.0%	20.7%	29.3%
Synedra	2.5	N.S.	76.0	99.4	208.0	185.6	142.2
		N.S.	25.2%	23.8%	37.0%	28.5%	28.6%
	5	N.S.	174.0	97.9	81.8	96.6	112.5
		N.S.	24.2%	16.4%	14.8%	20.1%	18.9%
	10	134.5	83.5	166.8	116.7	71.4	114.5
		23.3%	30.5%	31.7%	27.6%	19.6%	26.5%
	15	150.9	54.8	N.S.	73.2	109.7	97.1
		21.4%	31.7%	N.S.	37.8%	28.1%	29.8%

*N.S. means no sample was collected. Three dashes mean zero.

TABLE VI (Continued)

Organism	Depth in Feet	8-9	8-17	8-23	8-25	9-6	Mean
	20	257.4 36.8%	78.4 21.9%	56.8 17.4%	168.0 33.1%	112.4 25.2%	134.6 26.9%
	35	206.6 26.4%	156.2 20.6%	127.7 26.0%	126.8 24.0%	177.8 28.4%	159.0 25.1%
Unidentified Diatoms	2.5	N.S. N.S.	25.3 8.4%	65.9 15.8%	78.2 13.9%	148.5 22.8%	79.4 15.2%
	5	N.S. N.S.	71.3 9.9%	84.7 14.2%	163.6 29.6%	105.7 22.0%	106.3 18.9%
	10	64.8 11.2%	33.8 12.4%	90.5 17.2%	72.5 17.1%	74.8 20.6%	67.2 15.7%
	15	73.2 10.4%	12.6 7.3%	N.S. N.S.	38.8 20.0%	79.4 20.4%	51.0 14.5%
	20	69.8 10.0%	44.0 12.3%	59.5 18.2%	95.0 18.7%	104.7 23.5%	74.6 16.5%
	35	80.9 10.3%	125.6 16.5%	78.0 15.9%	105.7 20.1%	134.7 21.6%	104.9 16.9%
Cymbella	2.5	N.S. N.S.	25.3 8.4%	25.4 6.1%	86.5 15.4%	27.0 4.1%	41.0 8.5%
	5	N.S. N.S.	7.9 1.1%	66.1 11.1%	24.5 4.4%	27.2 5.7%	31.4 5.6%
	10	34.9 6.0%	26.7 9.8%	48.1 9.1%	22.1 5.2%	27.2 7.5%	31.8 7.5%

TABLE VI (Continued)

Organism	Depth in Feet	8-9	8-17	8-23	8-25	9-6	Mean
	15	64.0 9.1%	8.4 4.9%	N.S. N.S.	17.2 8.9%	28.0 7.2%	29.4 7.5%
	20	21.9 3.1%	19.3 5.4%	16.2 5.0%	23.1 4.6%	23.3 5.2%	20.8 4.7%
	35	26.9 3.4%	33.7 4.4%	26.0 5.3%	13.2 2.5%	26.2 4.2%	25.2 4.0%
Nevicula	2.5	N.S. N.S.	27.6 9.2%	42.8 10.3%	37.1 6.6%	84.4 13.0%	48.0 9.8%
	5	N.S. N.S.	29.0 4.0%	42.3 7.1%	32.7 5.9%	33.2 6.9%	34.3 6.0%
	10	34.9 6.0%	12.4 4.5%	23.2 4.4%	18.9 4.5%	27.2 7.5%	23.2 5.4%
	15	36.6 5.2%	19.0 11.0%	N.S. N.S.	6.5 3.4%	11.7 3.0%	1.8 5.7%
	20	48.0 6.9%	19.3 5.4%	N.S. 0%	28.3 5.6%	7.8 1.7%	20.7 3.9%
	35	21.0 2.7%	21.4 2.8%	35.5 7.2%	34.3 6.5%	39.9 4.8%	28.4 4.8%
Cocconeis	2.5	N.S. N.S.	2.3 .8%	1.2 .3%	4.1 .7%	6.7 1.0%	3.6 .7%
	5	N.S. N.S.	18.5 2.6%	7.9 1.3%	--- 0%	9.0 1.9%	8.9 1.5%
	10	5.0 .9%	12.4 4.5%	22.6 4.3%	12.6 3.0%	10.2 2.8%	12.6 3.1%

TABLE VI (Continued)

Organism	Depth in Feet	8-9	8-17	8-23	8-25	9-6	Mean
	15	45.7	8.4	N.S.	---	11.7	16.5
		6.5%	4.9%	N.S.	0%	3.0%	3.6%
	20	91.7	12.4	13.5	2.6	23.3	28.7
		13.1%	3.5%	4.1%	.5%	5.2%	5.3%
	35	24.0	91.9	14.2	21.1	43.0	38.8
		3.1%	12.1%	2.9%	4.0%	6.9%	5.8%
Gomphonema	2.5	N.S.	9.2	39.3	16.5	10.1	18.8
		N.S.	3.1%	9.4%	2.9%	1.6%	4.3%
	5	N.S.	31.7	18.5	12.3	3.0	16.4
		N.S.	4.4%	3.1%	2.2%	.6%	2.6%
	10	---	1.8	10.5	3.2	---	3.1
		0%	.7%	2.0%	.8%	0%	.7%
	15	18.3	---	N.S.	---	2.3	4.1
		2.6%	0%	N.S.	0%	.6%	.8%
	20	4.4	11.0	18.9	23.1	11.6	13.8
		.6%	3.1%	5.8%	4.6%	2.6%	3.3%
	35	47.9	15.3	28.4	18.5	18.7	23.8
		6.1%	2.0%	5.8%	3.5%	3.0%	4.1%

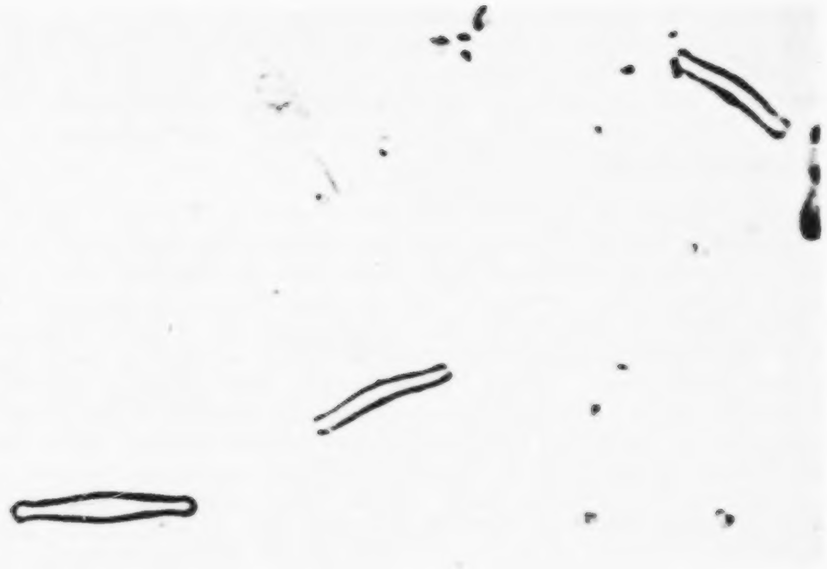

Figure 5. Achnanthes microcephala

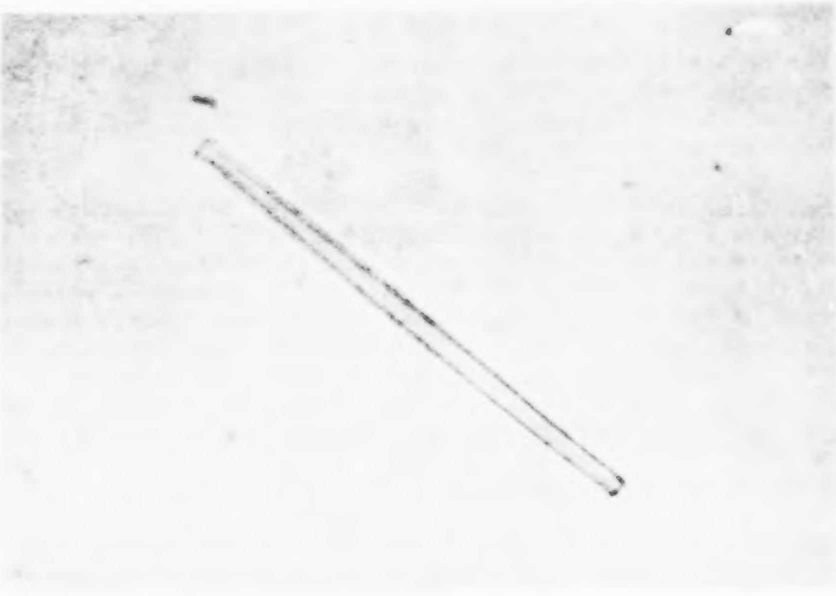

Figure 6. Synedra acus

According to Smith (1950) *Acnanthes* is found in both salt and fresh water and is usually attached by means of a gelatinous stalk to some firm object. About a dozen species have been reported for the United States. In 1966 on August 17, this genus reached its maximum in Stony Point Bay in terms of absolute numbers (356,500/cm^2) and percentage of the total growth (49.7 per cent). The species was *Acnanthes microcephala*.

Synedra (Figures 5 and 6) was the second most common organism and it reached a maximum of 257,400 per square centimeter on August 9 at a depth of twenty feet. At five feet, the percentage contribution of *Synedra* to the total remained low throughout the season in comparison to the other depths. The fact that *Achnanthes* was higher than normal at this depth suggests an upset in the balance evidently existing between these two genera. Smith (1950) states that *Synedra* occurs in a variety of habitats. The smaller species are usually sessile and form a brownish-green layer on stones and woodwork in running water while the larger species are either free-floating or occur epiphytically in lakes. Twenty-five species occur in the United States. The predominant species of *Synedra* found in the Stony Point Bay periphyton is shown in Plate 2.

The unidentified organisms category listed in Table VI include small pieces of broken organisms, atypical forms which were impractical to identify, and a number of organisms which were "naviculoid" in appearance but which could not with certainty be assigned to the genus *Navicula*.

The remaining diatoms in Table VI, *Cymbella*, *Navicula*, *Cocconeis*, and *Gomphonema*, each comprise an average of less than seven per cent of the total at all depths. Figures 8 through 15 are photomicrographs of common species from these four genera.

Cymbella, with an average mean percentage for all depths of 6.3 per cent, was the fourth most common organism. Smith (1950) states that this organism may be either free-floating or sessile. The sessile species may be found singly at the tip of a stout gelatinous stalk or may occur grouped seriately within branched gelatinous tubes. A typical *Cymbella ventricosa* tube and its included organisms are shown in Figure 8. *Cymbella lanceolate* (Figure 9) typically grows at the tip of a stalk, which, in this case, has been incinerated. *Cymbella*, like *Navicula*, *Cocconeis*, and *Gomphonema*, shows no marked seasonal variations in Stony Point Bay. However, the means of the numbers and percentages at each depth indicate that *Cymbella* decreases with increasing depth.

Navicula (Figures 10 and 11) comprises on the average 6.1 per cent of the total at all depths and is the only one of the seven organisms listed which is usually free-floating. *Navicula* is motile and probably moves at will among the other members of the attached periphyton. Strictly speaking, organisms that are not attached but live with the periphyton constitute a part of the merophyton. *Navicula*, like *Cymbella*, seemed to decrease as the depth of the water increased.

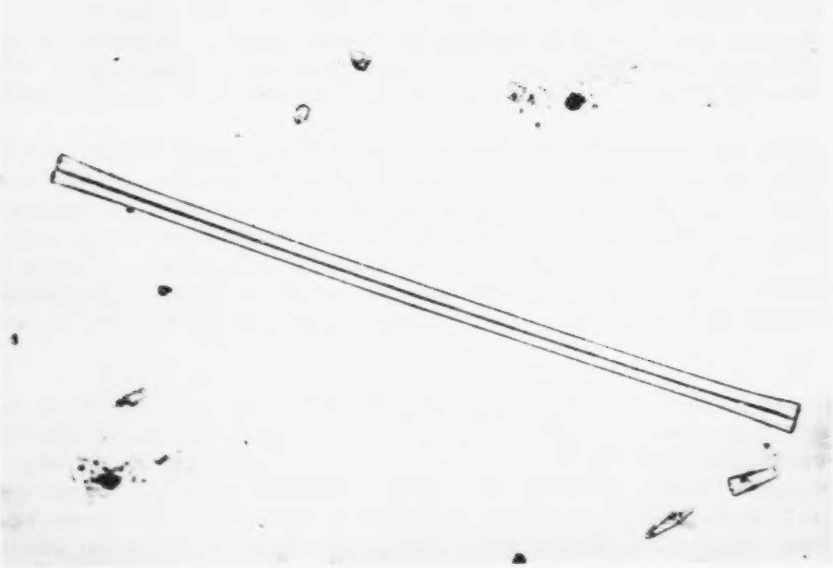

Figure 7. Synedra ulna

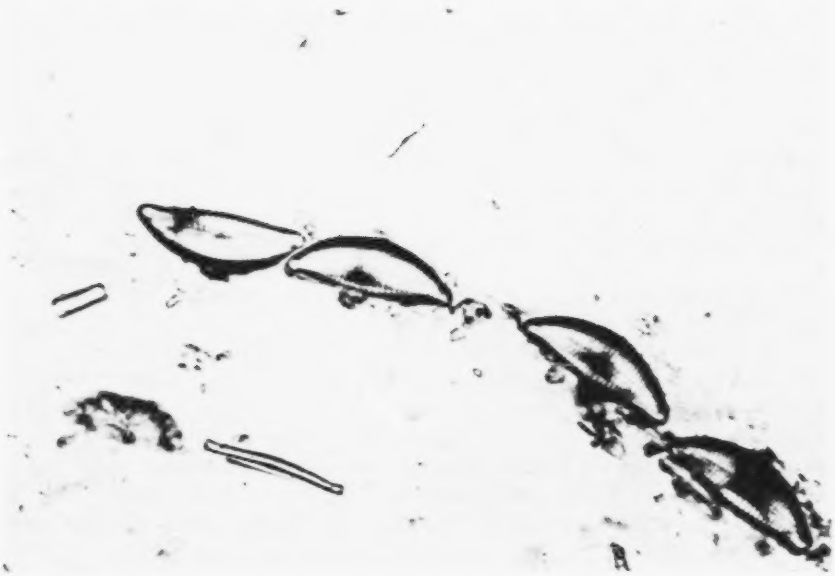

Figure 8. Cymbella ventricosa

Cocconeis, with an average mean percentage at all depths of 3.7 per cent, was the sixth most abundant organism. Four species of this predominantly marine genus occur in fresh water. All grow attached, with the hypotheca flattened against the substratum. Figures 12 and 13 show two species commonly found in Stony Point Bay. *Cocconeis*, unlike *Cymbella* and *Navicula*, was more common in samples from deeper water.

Gomphonema comprised on the average 2.6 per cent of the total count at all depths. According to Smith (1950), the frustules "are usually epiphytic and borne at the tips of a dichotomously branched system of gelatinous stalks." This method of attachment is illustrated by Figure 14. Here, the organisms appear in girdle view. Figure 15 represents the valve view. *Gomphonema* occurred in highest percentages at 2.5 and thirty-five feet. The minimum occurred at ten and fifteen feet.

The dry weights of the 1966 samples are presented in Table VII. Results are expressed as milligrams of dry weight per square centimeter of rock surface. Because the samples used for counting and those used for the weight determinations were taken from the same periphyton-water suspension, each weight is representative of a corresponding count. The weights, according to the mean weight at each depth, were lowest at 2.5 feet and gradually reached their peak at fifteen feet. The variations of the weights, if viewed alone, would be expected on the basis of the factors already discussed, namely, dislodgement of the periphyton by waves in the shallow water and lower numbers due to the decrease in light and temperature in the deeper water. The fact that the counts (Figure 4 and Table V) do not correlate with their corresponding dry weights (Table VII) may be due to the variation in the sizes of the individual organisms at each depth. Thus, if the total count at a particular depth is high and the corresponding dry weight is low, one could surmise that the individual organisms were of a small size. By the same token, larger organisms in smaller numbers could cause a higher dry weight. This disparity might also be explained by the presence of varying amounts of sand in the periphyton-water suspensions or by the presence of empty diatom frustules. Both of these factors could cause fluctuations in the dry weights.

It is most probable that rough water dislodged and suspended both periphyton and sand in Stony Point Bay. The sand, of course, would settle rapidly on the rocks and is probably included in the dry weights, while some of the periphyton, which would take longer to settle out, was carried away by the current. This theory explains why the weights were high when the counts were low and *vice versa*. In an attempt to determine why the counts did not correlate with the dry weights the methods were modified in 1967. In that year, the ash-free dry weight, or organic weight, of the periphyton was determined.

On the basis of the average of the 1966 mean dry weights for all of the depths, the total biomass, or standing crop, of the Stony Point Bay periphyton was calculated to be 37.1 tons (104 g./m.^{2}). The fact

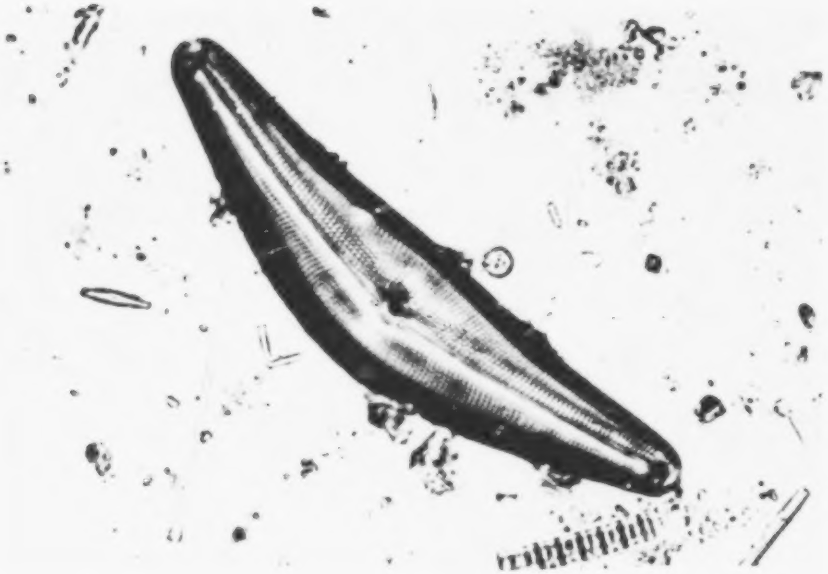

Figure 9. Cymbella lanceolata

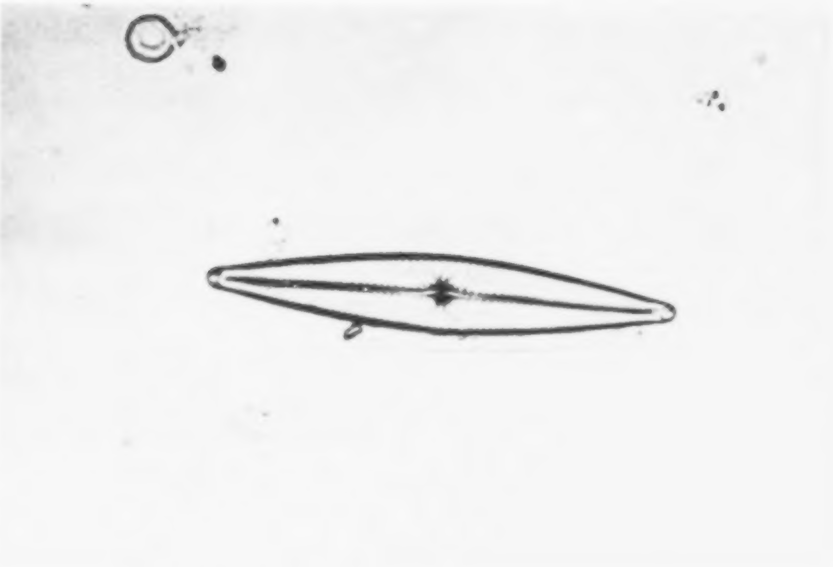

Figure 10. Navicula radiosa

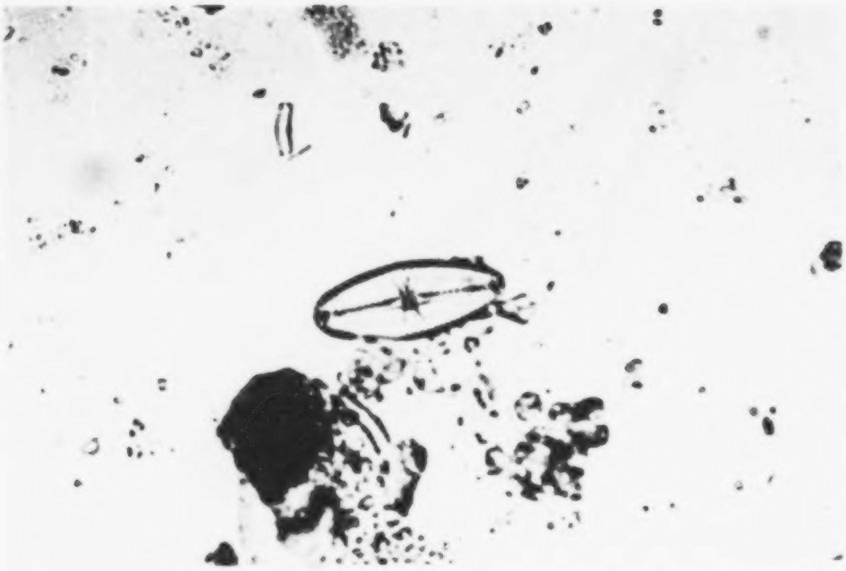

Figure 11. Navicula reinhardii

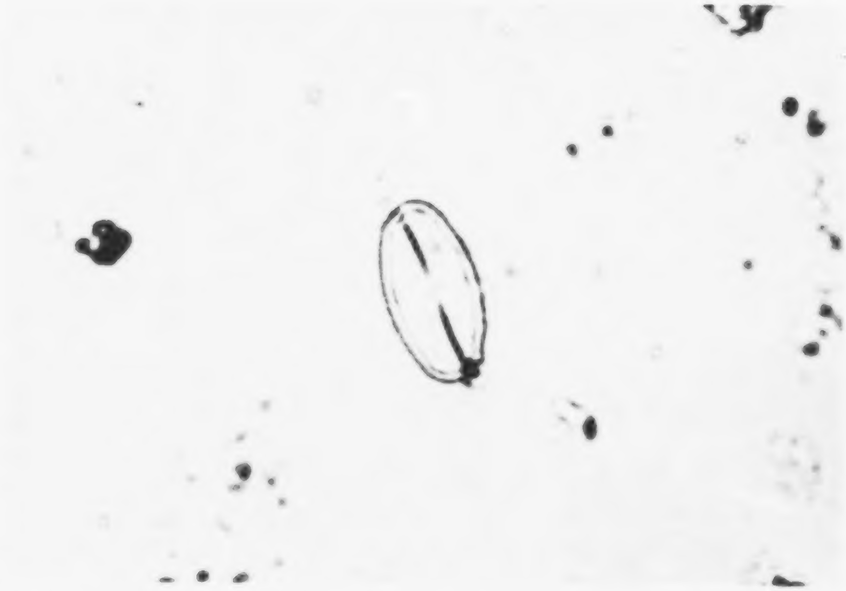

Figure 12. Cocconeis flexella

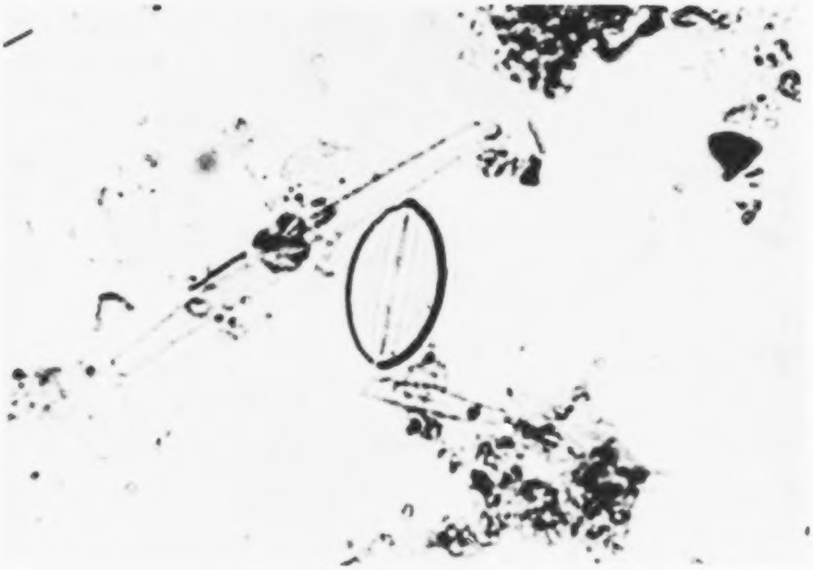

Figure 13. Cocconeis placentula

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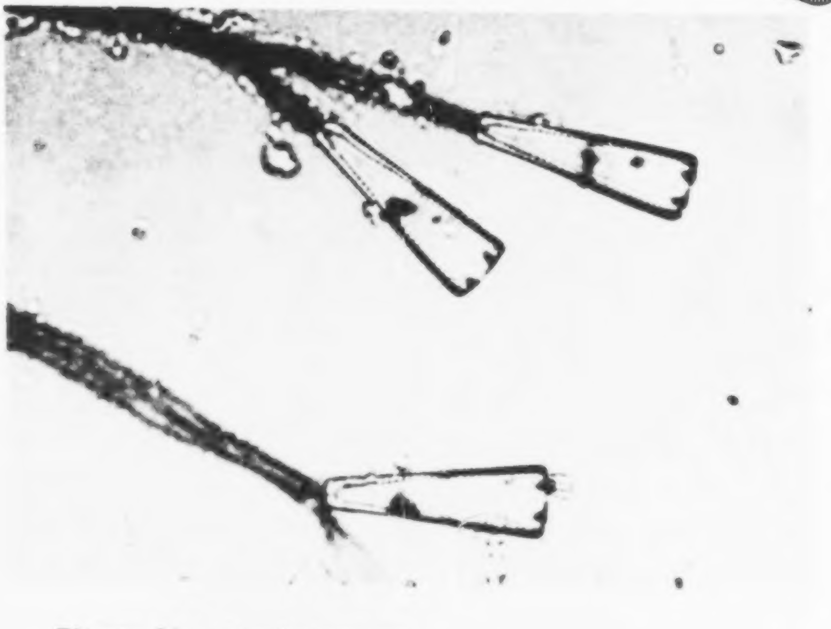

Figure 14. Gomphonema sp.

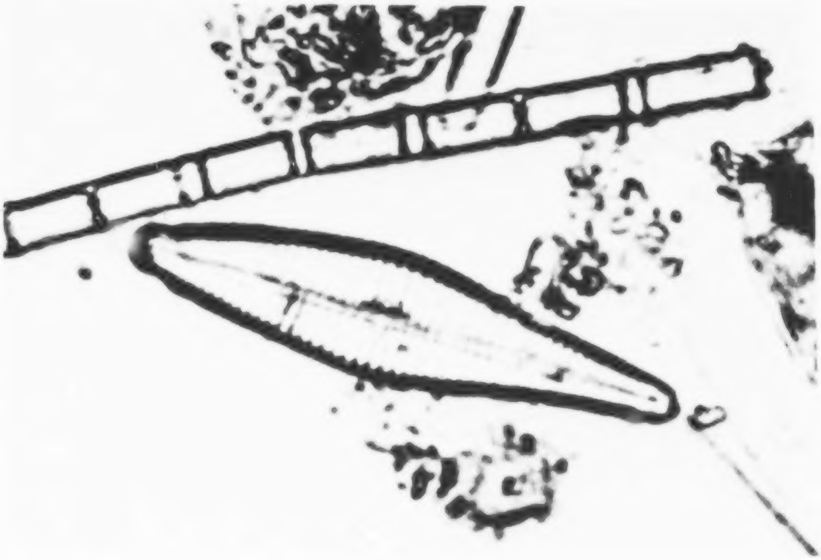

Figure 15. Gomphonema olivaceum

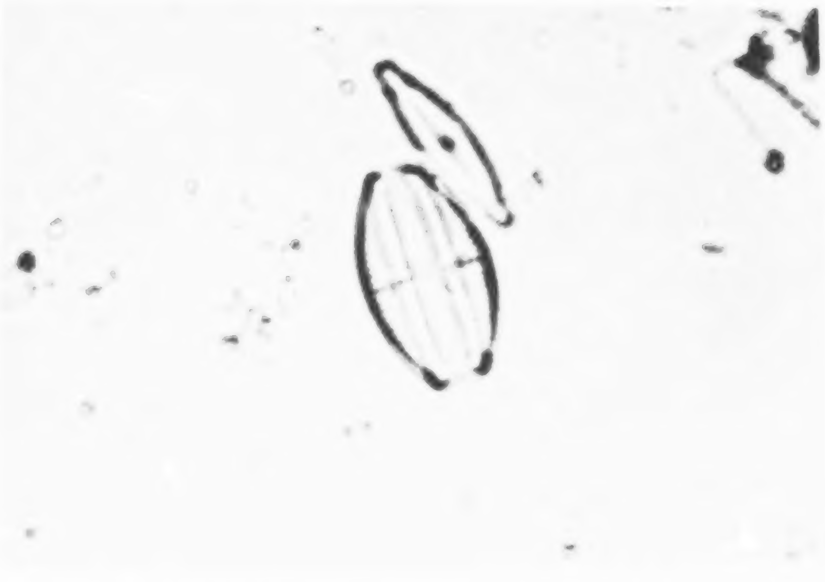

Figure 16. Amphora ovalis v. pediculus

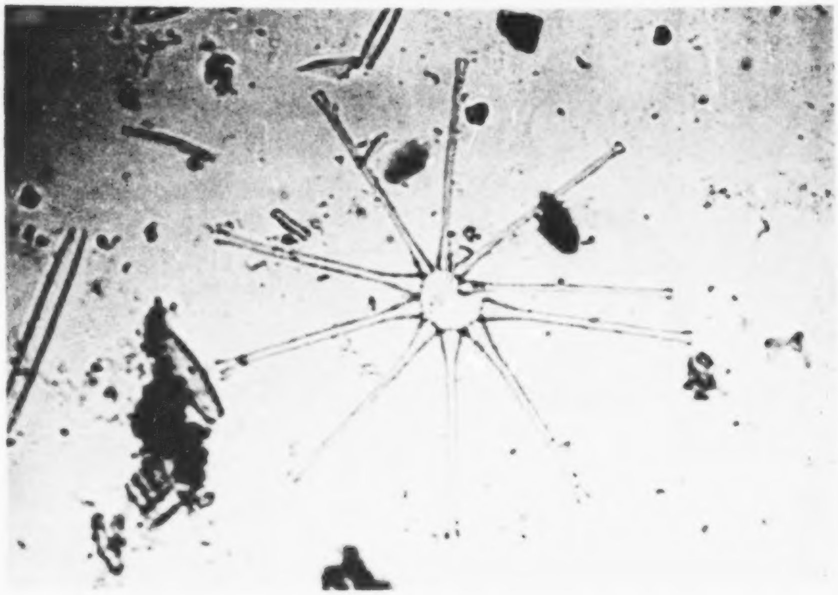

Figure 17. Asterionella formosa

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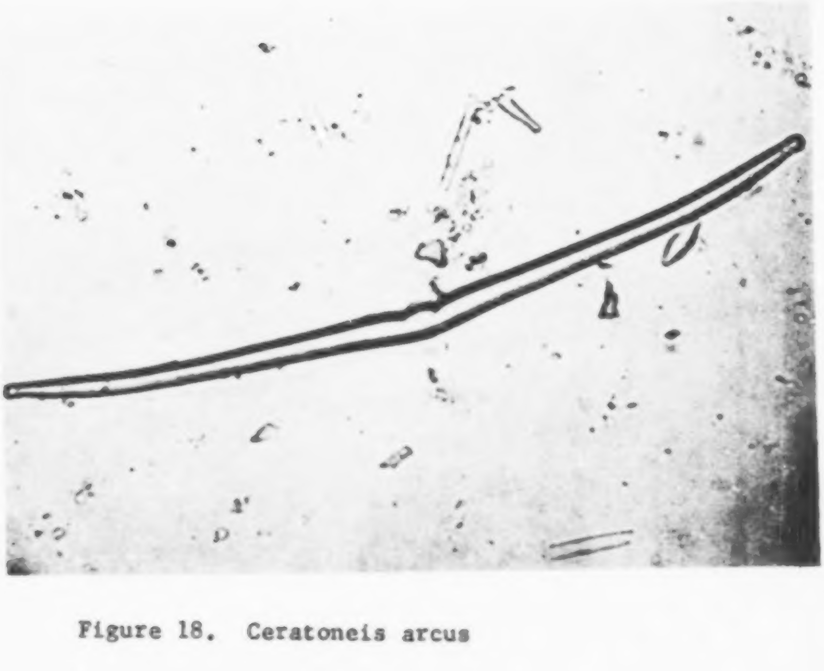

Figure 18. Ceratoneis arcus

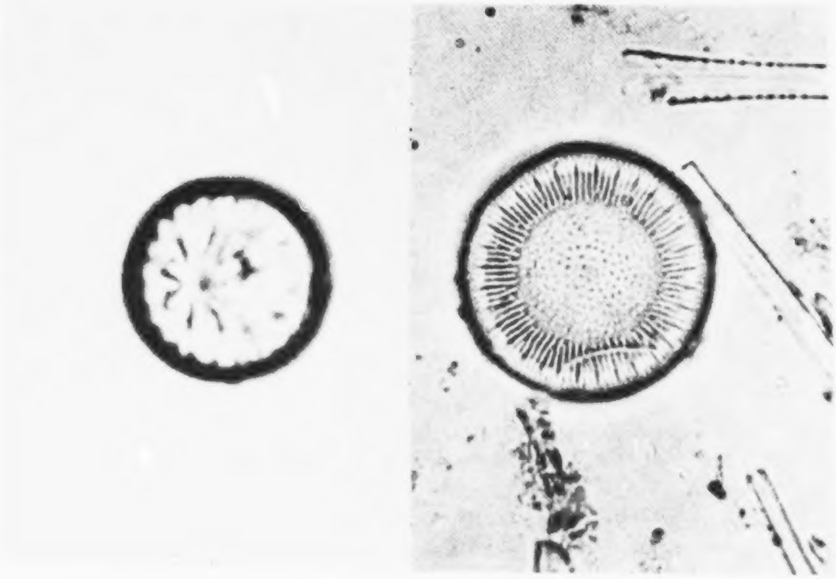

Figure 19. Cyclotella sp.
Large Cyclotella bodanica Small Cyclotella antiqua

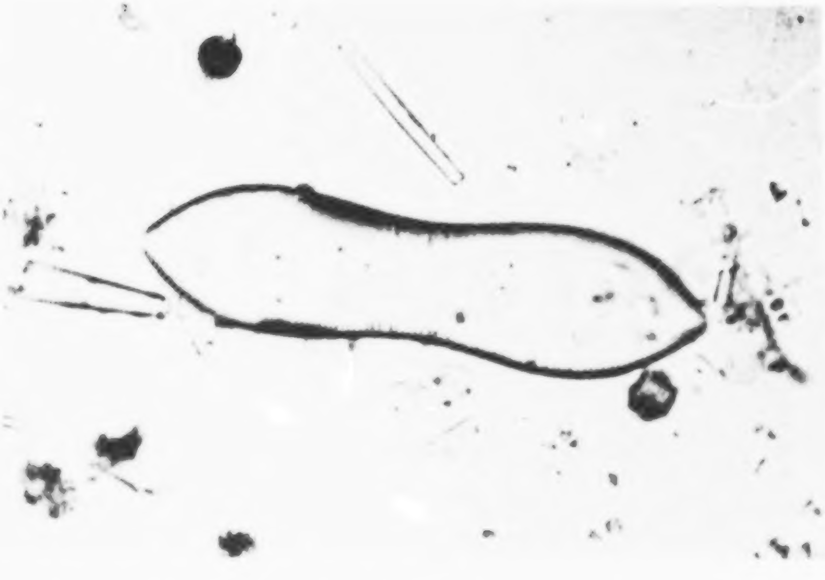

Figure 20. Cymatopleura solea

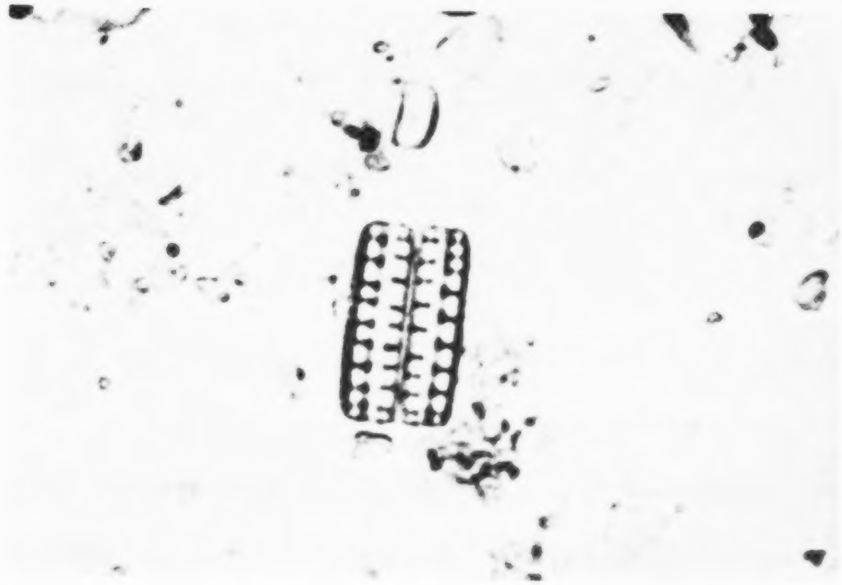

Figure 21. Denticula thermalis

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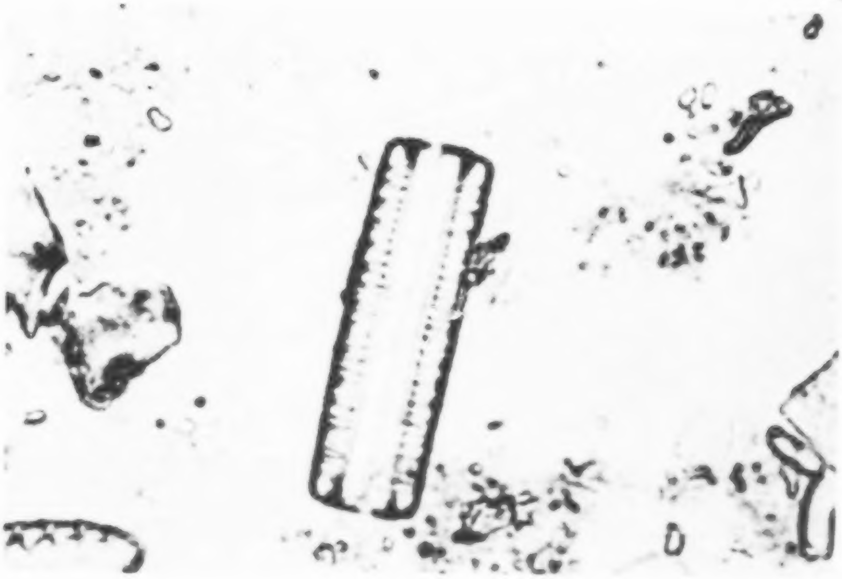

Figure 22. Diatoma vulgare

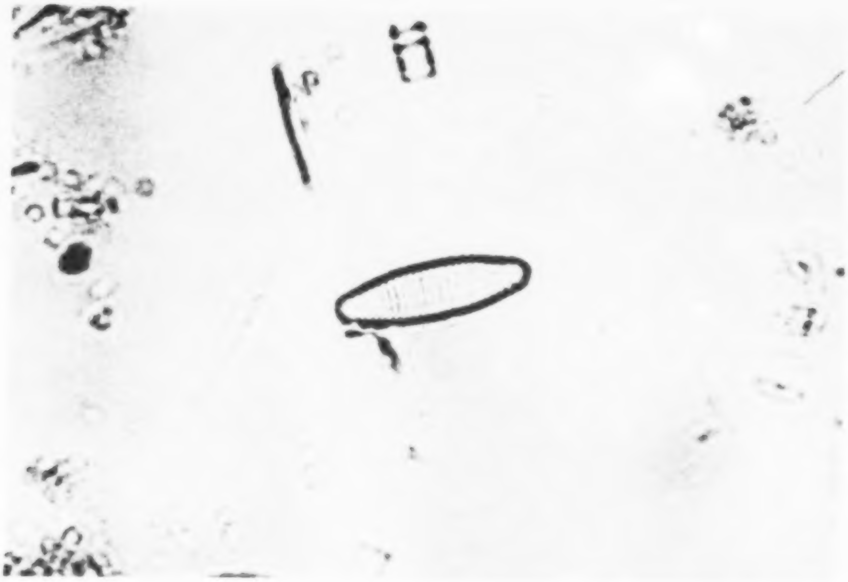

Figure 23. Diatoma vulgare

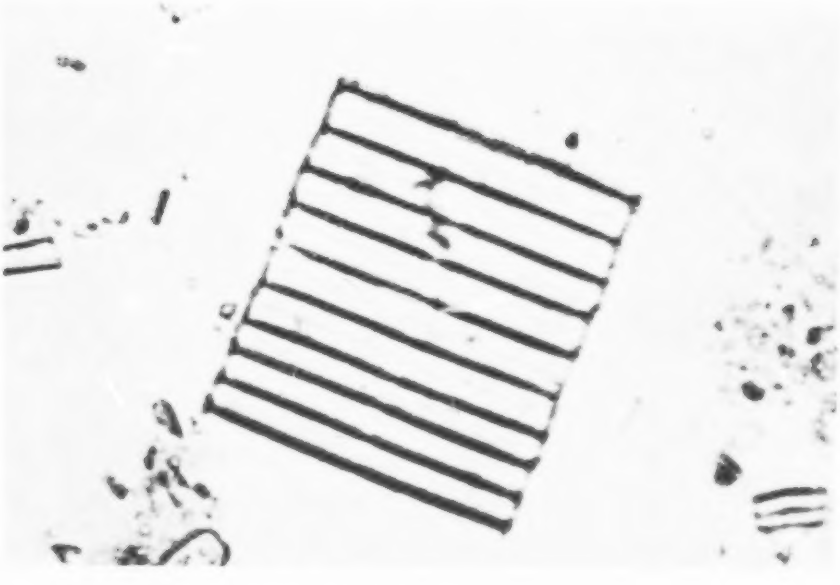

Figure 24. Fragilaria capucina

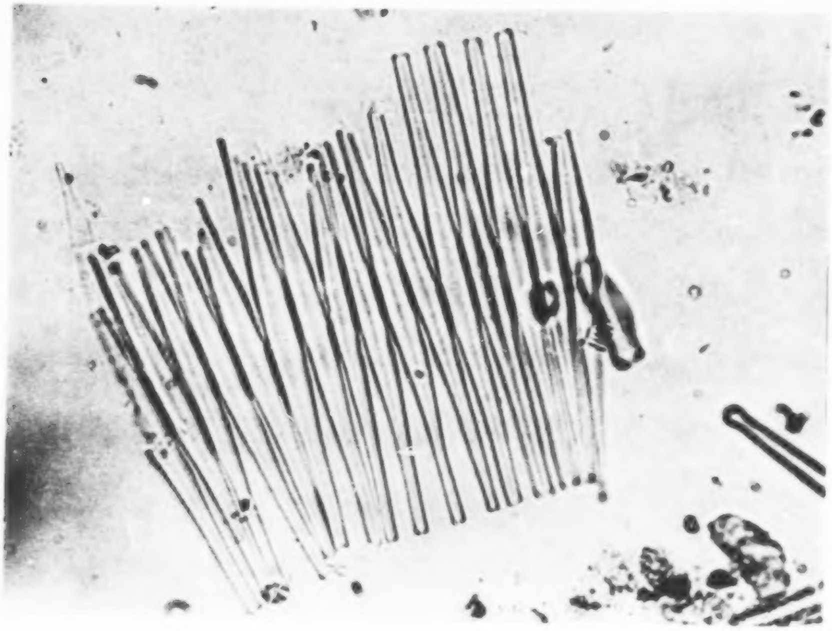

Figure 25. Fragilaria crotonensis

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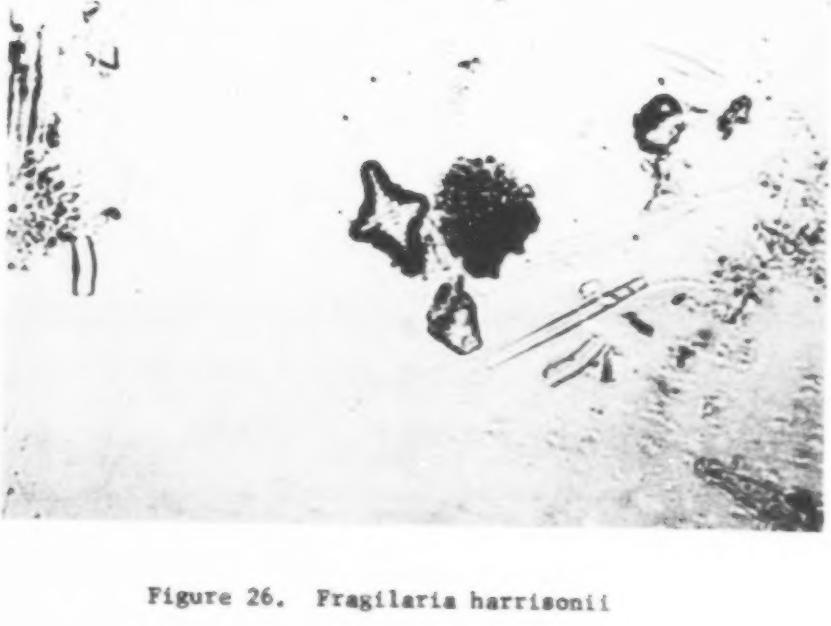

Figure 26. Fragilaria harrisonii

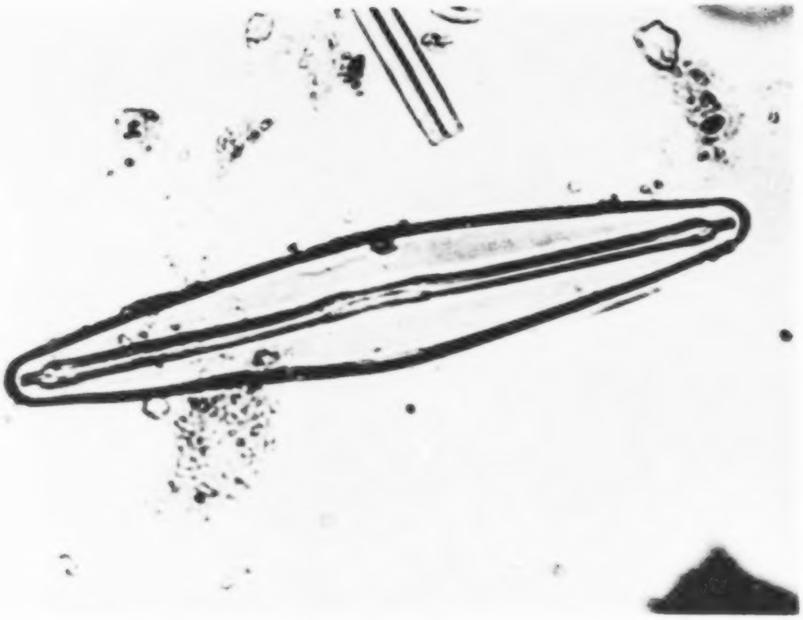

Figure 27. Frustulia viridula

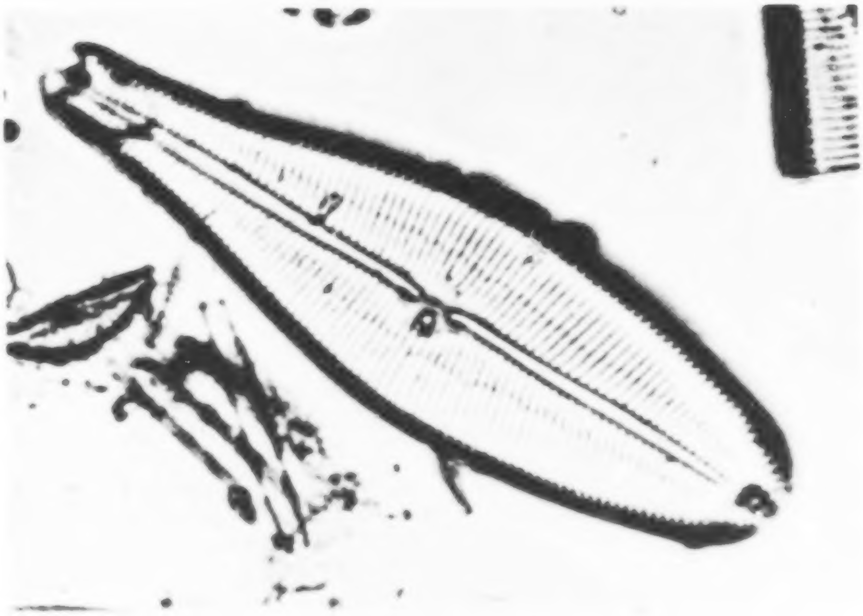

Figure 28. Gomphoneis herculeana

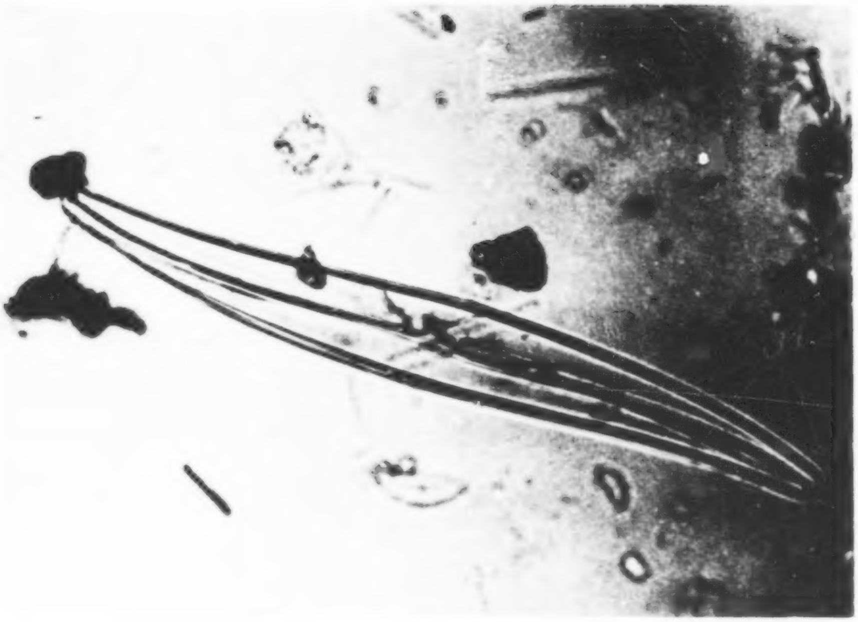

Figure 29. Gyrosigma attenuatum

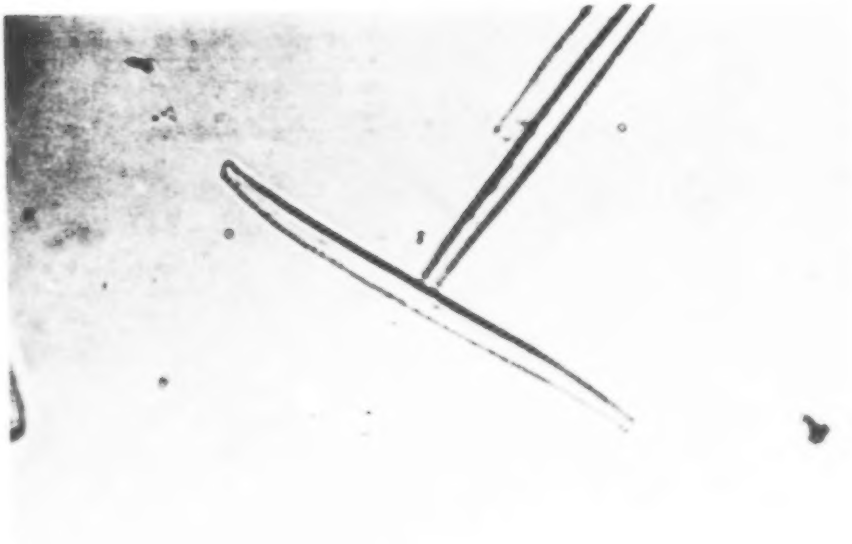

Figure 30. Nitzschia vermicularis

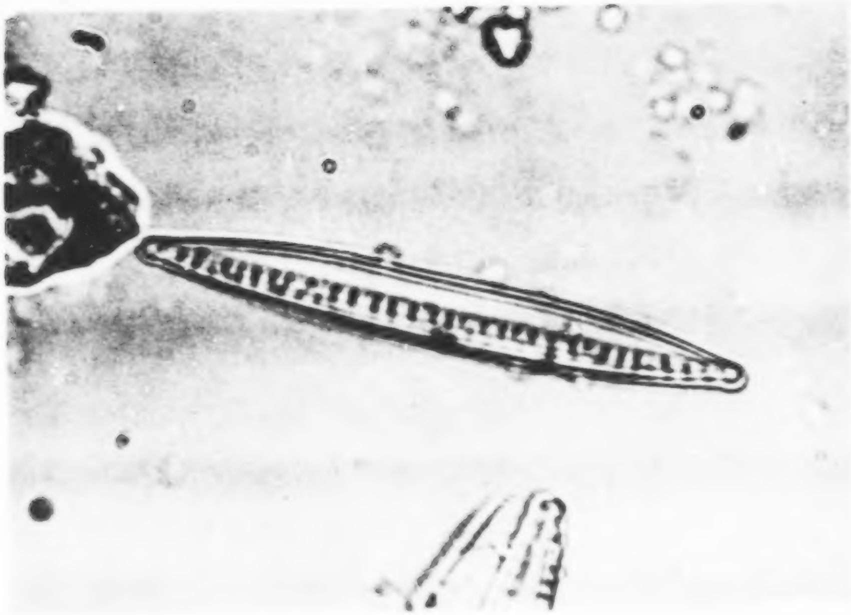

Figure 31. Nitzschia palea

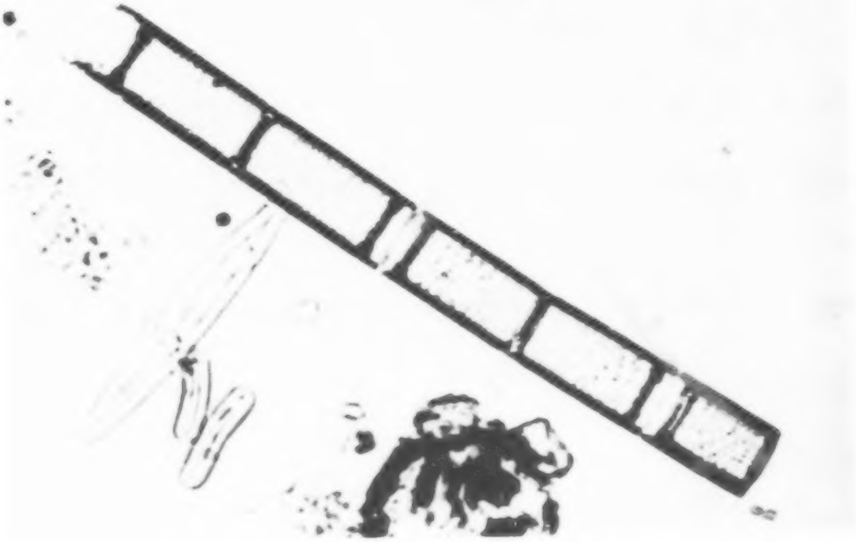

Figure 32. Melosira granulata

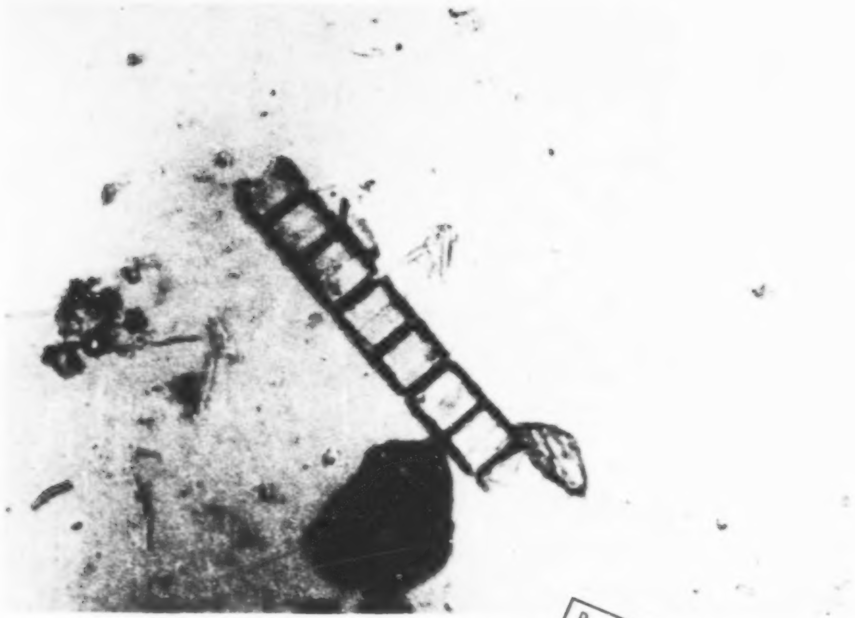

Figure 33. Melosira varians

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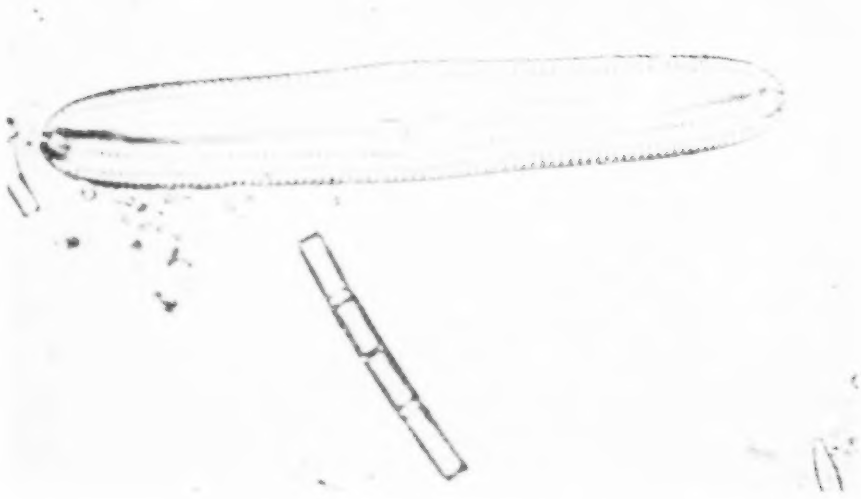

Figure 34. Pinnularia viridis

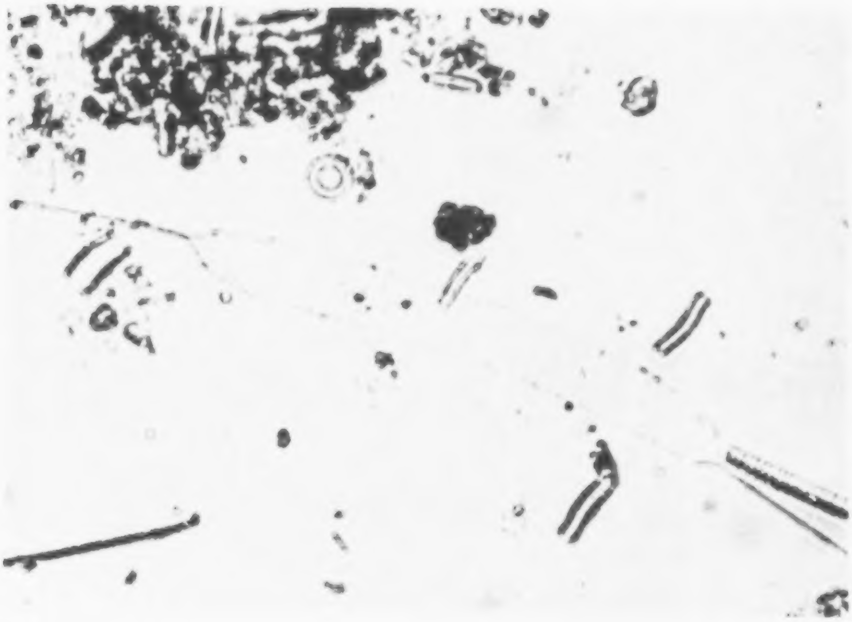

Figure 35. Rhizosolenia eriensis

Figure 36. Rhoicosphenia curvata

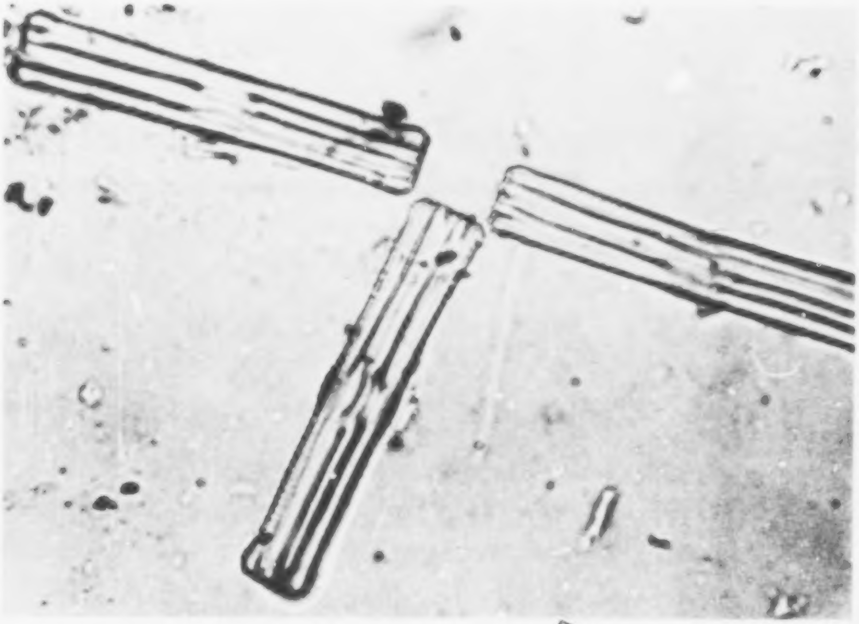

Figure 37. Tabellaria fenestrata

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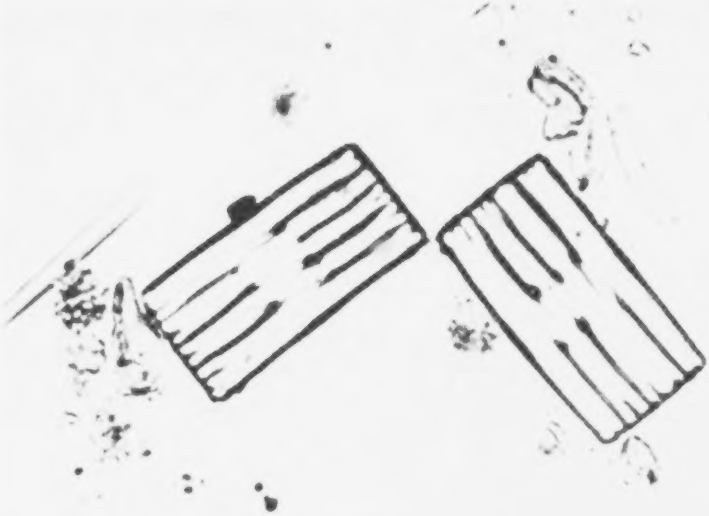

Figure 38. Tabellaria flocculosa

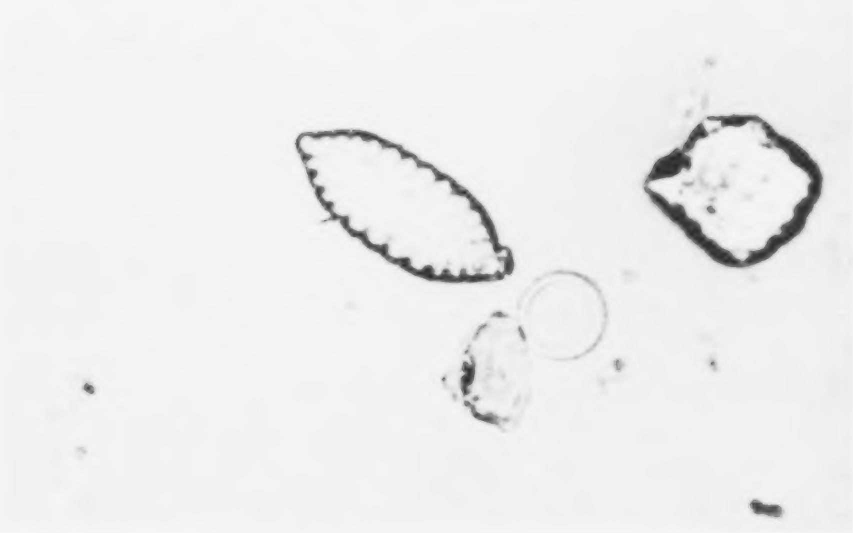

Figure 39. Surirella angustata

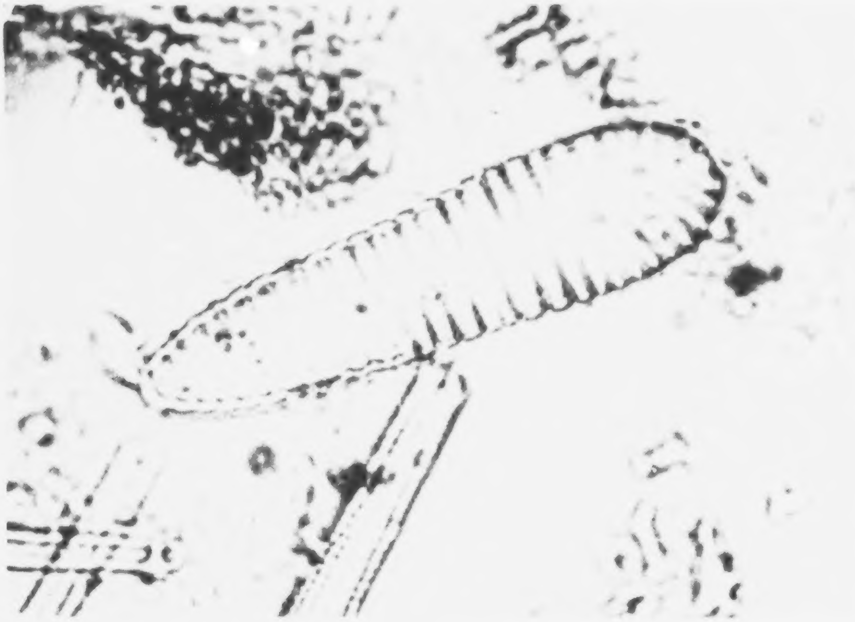

Figure 40. Surirella ovata v. pinnata

that this figure is lower than the comparable figure (54.4 tons or 153 g./m.^{2}) for 1965 is probably due to the rough weather of 1966. Even though six depths were sampled during 1966, as compared to three for 1965, the average depth sampled was just about the same for the two years.

The results of 1967 are presented in three sections. The first deals with the naturally occurring periphyton of Stony Point Bay. The second section is concerned with regrowth studies made in the same area while the third includes the results of studies conducted in areas other than Stony Point Bay along Lake Superior's north shore.

TABLE VII

NATURALLY OCCURRING PERIPHYTON DRY WEIGHTS AT THE STANDARD DEPTHS, STONY POINT BAY, LAKE SUPERIOR, 1966
MILLIGRAMS PER SQUARE CENTIMETER
OF ROCK SURFACE.

	Depth in Feet					
Date	2.5	5	10	15	20	25
8-9	N.S.*	N.S.	19.7	30.0	32.0	9.9
8-17	7.5	15.1	5.1	6.0	12.4	24.3
8-23	2.5	4.8	7.3	N.S.	2.1	5.3
8-25	10.0	3.1	6.0	10.0	11.0	9.2
9-6	6.0	5.4	13.0	10.2	9.5	9.7
Mean	6.5	7.1	10.2	14.0	13.4	11.6

*N.S. means no sample was collected.

Naturally occurring periphyton, Stony Point Bay.

During 1967, routine sampling was carried on between July 11 and September 15. An additional sampling trip was made on November 10. From July 11 to November 10, samples were collected on seventeen days. On each day, three rocks were obtained from each of the six standard sampling depths (2.5, 5, 10, 15, 20 and 35 feet). A total of 306 rocks was collected.

The numbers of organisms found at each depth are presented in Figure 41. Each point represents the mean count of seventeen samples collected from one particular depth during the sampling season. The means, rounded off to the nearest ten thousand, range from a maximum of 2,116,000 per square centimeter at 2.5 feet to a minimum of 1,034,000 per square centimeter at thirty-five feet. The downward trend in the counts as the depth increases is logical in view of certain facts. With increasing depth, light penetration is diminished and the temperature drops. The decrease in these two factors results in the generally lower periphyton populations which are shown in Figure 41. A mean of the counts at all depths is 1,470,000 organisms per square centimeter of rock surface. The mean of the 1967 counts for all depths was three times as high as the comparable figure for 1966. This threefold differential did not hold true at each depth, thus accounting for the difference in the shape of the curves. The greatest differences occurred in shallow water. At 2.5 feet, the 1967 mean count was more than four times as high as the 1966 mean count at the same depth. At five and ten feet, the 1967 means were greater than three times those of the comparable 1966 means. At fifteen and twenty feet, the 1967 mean counts were less than three times those of 1966, while the 1967 count at thirty-five feet was less than twice as high as the 1966 thirty-five foot mean count. These findings further substantiate the hypothesis that bad weather adversely affects periphyton growth, particularly in shallow water. The summer of 1967 was characterized by ideal weather conditions. High numbers of organisms were present that year because violent storms did not dislodge the periphyton nor stir up the bottom to produce deleterious turbidity. Climatological records show that during the 1967 sampling season (sixty-seven days) east winds occurred on only eleven days, or sixteen per cent of the time. No northeast winds occurred. In contrast, east and northeast winds occurred during thirty-nine per cent of the 1966 sampling season. While it is felt that the differing weather conditions which occurred during the two years are primarily responsible for the variations in the counts, the twofold decrease in the counts at thirty-five feet may have been caused by factors other than, or in addition to, the weather.

The variations in the total counts of organisms according to date are presented in Figures 42 through 47. Since, in this case, each count is an actual count and not a mean these curves show greater variation than does Figure 41. However, the figures reflect the general decrease with depth shown by Figure 41. This can readily be seen if the graphs are superimposed and the area below each curve is inspected. The greatest variation is shown in the counts from samples obtained from shallow water.

While it is impossible to explain precisely the causes for each dip and rise in these six curves, it is possible to surmise the reason for the similarity between the curves for the four relatively shallow depths (2.5, 5, 10, and 15 feet). A plausible explanation can also be offered for the similarity between the twenty and the thirty-five foot curves. The variability exhibited by the shallower water counts (Figures 42-45) is probably due to the effect of wave action upon the

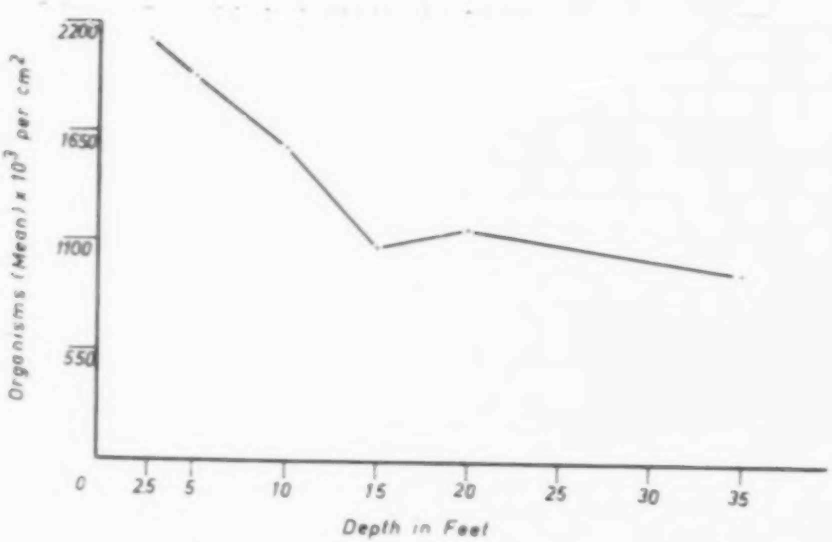

Figure 41. Mean total counts of naturally occurring periphyton at the standard sampling depths, Stony Point Bay, Lake Superior, 1967.

periphyton. Each peak represents a renewal of growth or settling of organisms that took place after some climatic disturbance. The high mean of the counts in the shallow water show that the growth was never seriously reduced by the effects of waves or currents. The fact that the peaks and dips correspond, in general, at the different depths supports this weather hypothesis. The progressive increases exhibited by Figures 46 and 47 (twenty and thirty-five feet) are probably indicative of a true rising seasonal trend, which reached a maximum on September 5. The minor hydraulic disturbances causing deviations in the counts of the shallow water samples were probably not strong enough to affect growth in the deeper water. The dip in the counts at twenty and thirty-five feet on August 28 may have been caused by a deep current, which may have also been responsible for the periphyton reduction in the shallower water (2.5 and 10 feet) on the same date. Such a current could be produced in a number of ways. In this instance, it could be that strong shifting winds produced water movement which swept away part of the periphyton. Weather data during the period in question tend to support this view. Intermittent rainstorms with attendant winds of twenty-five miles an hour or greater were recorded on August 24 through August 26. At the onset, the winds were from the south. There was then a gradual shift to the southwest and finally, to the northwest. However, the lower count at twenty feet on August 17, which was not accompanied by coincidental decreases at thirty-five feet and at the shallow water stations, must be ascribed to a local current of unknown origin.

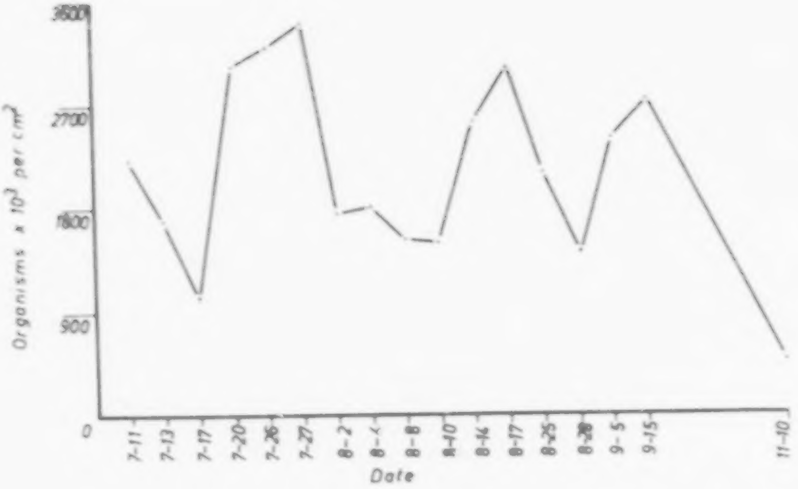

Figure 42. Naturally occurring periphyton, total counts at 2.5 feet, Stony Point Bay, Lake Superior, 1967.

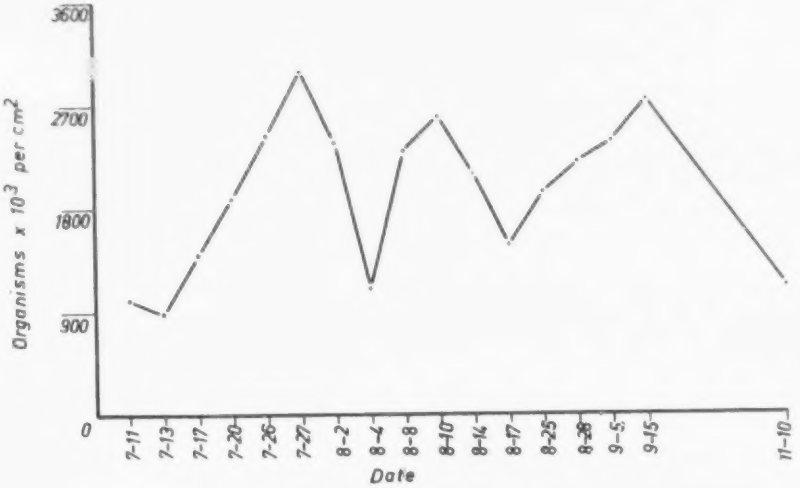

Figure 43. Naturally occurring periphyton, total counts at 5 feet, Stony Point Bay, Lake Superior, 1967.

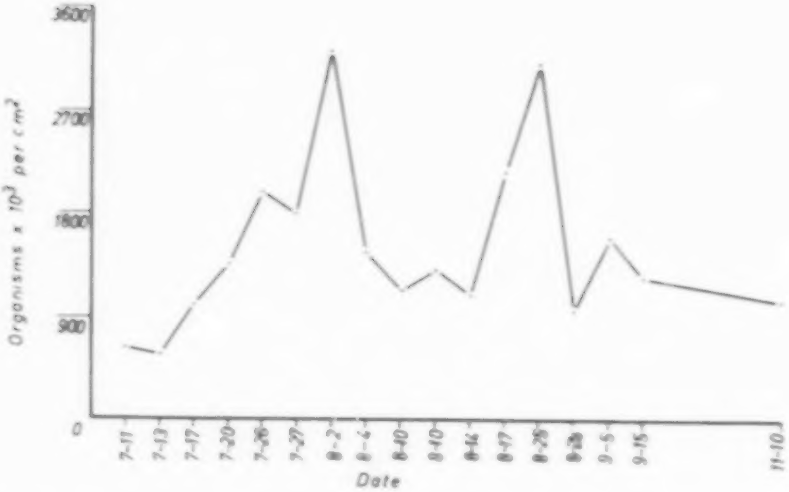

Figure 44. Naturally occurring periphyton, total counts at 10 feet, Stony Point Bay, Lake Superior, 1967.

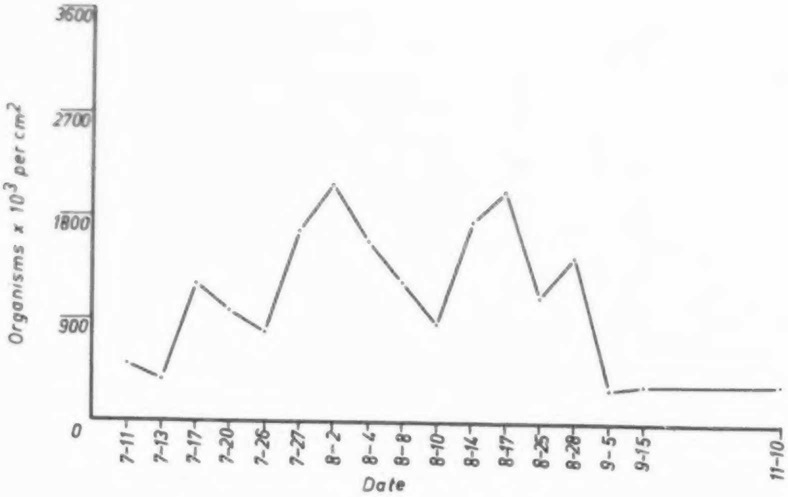

Figure 45. Naturally occurring periphyton, total counts at 15 feet, Stony Point Bay, Lake Superior, 1967.

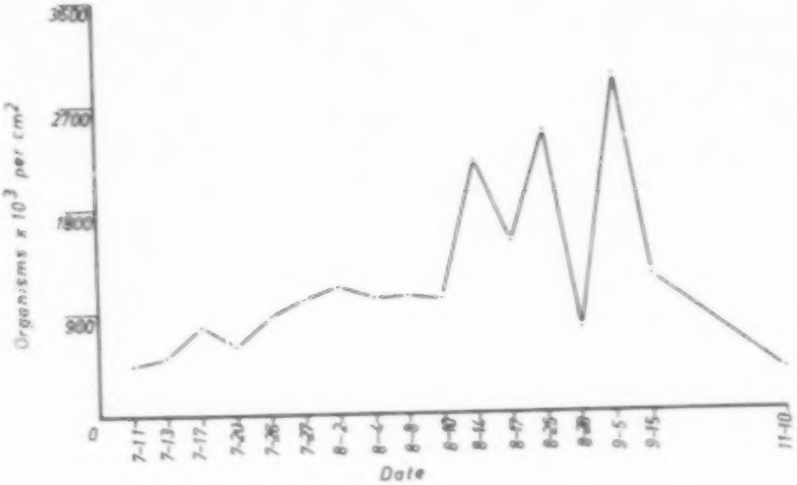

Figure 46. Naturally occurring periphyton, total counts at 20 feet, Stony Point Bay, Lake Superior, 1967.

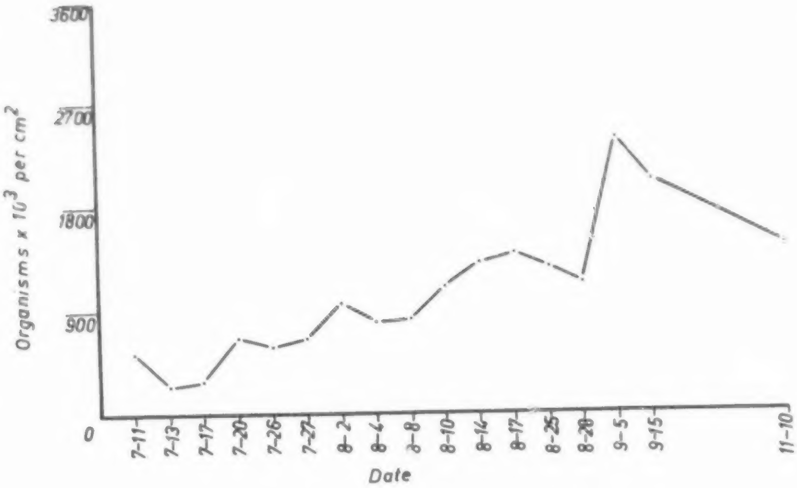

Figure 47. Naturally occurring periphyton, total counts at 35 feet, Stony Point Bay, Lake Superior, 1967.

A checklist of the organisms encountered while making the above counts is presented in Table 8. The total number of genera observed was thirty-eight. Sixty-eight per cent, or twenty-six genera, belong to the phylum Chrysophyta. Only one of these twenty-six genera, *Dinobryon*, is not a diatom. There were seven genera of green algae and five blue-green algae. Only these three phyla were represented. The checklist can be broken down further into sixty-one recognized species. Of the sixty-one species, forty-seven (seventy-seven per cent) were diatoms. Eight species of Chlorophyta and five species of Cyanophyta are reported.

Fourteen more genera of naturally occurring periphyton were encountered during 1967 than were found in the 1966 samples. In both years, however, the proportion of diatom genera to greens and blue-greens remained constant. The twenty-four genera encountered during 1966 (Table IV) were also present in 1967. The fourteen additional genera found in 1967 were: Chrysophyta - *Ceratoneis*, *Frustulia*, *Gomphoneis*, *Gyrosigma*, *Pinnularia*, *Rhoicosphenia*, and *Stauroneis*; Chlorophyta - *Cladophora*, *Pediastrum*, and *Spirogyra*; Cyanophyta - *Anabaena*, *Lyngbya*, *Oscillatoria*, and *Raphidiopsis*.

The number of organisms found is indicated by the mean total counts as shown in Figure 41. It will be noted that the means of the totals are used as points on the curve in this figure whereas the means of the total at each depth are plotted in Figures 42 through 47.

In all cases, Chrysophytes were by far the most abundant organisms, ranging from a minimum of 88.2 per cent of the total at twenty feet on September 15 to 100 per cent of the total in samples collected on November 9 at 2.5, 15 and 35 feet and on July 17 at 2.5 feet. With the one exception indicated, Chrysophytes always comprised at least 90% of the total population.

Chlorophytes, or green algae, were found in only 73 of 102 samples, or 71 per cent of the time. Blue-greens were more abundant and occurred in 87 per cent of the samples.

When results from the years 1966 and 1967 were compared it was found that the Chrysophytes were the predominant forms during both years. This was true for every sample from every depth. In many instances diatoms comprised the entire population and *Dinobryon* was the only genus of the *Chrysophyta* observed which was not a diatom.

The phyla Chlorophyta and Cyanophyta showed some variations in frequency of occurrence for the two year period. In 1966, greens were found in forty per cent of the samples, as contrasted with sixty-seven per cent in 1967. A similar rise in the blue-greens occurred during 1967. In 1966, the Cyanophytes were represented only by *Merismopedia*, which was present thirty-seven per cent of the time, whereas five genera of blue-greens occurred in 1967. Cyanophytes, in that year, were seen in eighty-seven per cent of the samples.

TABLE VIII

ORGANISMS OBSERVED IN NATURALLY OCCURRING PERIPHYTON, STONY POINT BAY, LAKE SUPERIOR, 1967.

- Phylum Chrysophyta
  - Class Bacillariophyceae
    - *Achnanthes microcephala* (Kuetzing) Cleve +
    - *Amphora ovalis* Kuetzing *+
    - *Amphora normani* Rabenhorst *
    - *Asterionella formosa* Hassall +
    - *Ceratoneis arcus* (Ehrenberg) Kuetzing +
    - *Cocconeis* group:
      - *C. flexella* (Kuetzing) Cleve +
      - *C. pediculus* Ehrenberg
      - *C. placentula* Ehrenberg +
    - *Cyclotella antiqua* Wm. Smith * +
    - *Cyclotella* group:
      - *C. bodanica* Eulenstein var. *michiganensis* Skvortzow +
      - *C. meneghiniana* Kuetzing
      - *C. michiganiana* Skvortzow
    - *Cymatopleura solea* (Brebisson) Wm. Smith* +
    - *Cymbella* group A:
      - *C. cistula* (Hemprich) Grunow
      - *C. lanceolata* (Ehrenberg) Van Heurck +
    - *Cymbella* group B:
      - *C. ventricosa* Kuetzing +
      - *C. amphicephala* Naegeli
    - *Denticula thermalis* Kuetzing +
    - *Diatoma elongatum* C.A. Agardh var. *tenuis* (Agardh) Van Heurck
    - *Fragilaria capucina* Desmazieres +
    - *Fragilaria crotonensis* Kitton * +
    - *Fragilaria harrisonii* (Wm. Smith) Grunow* +
    - *Frustulia viridula* (Brebisson) DeToni +
    - *Gomphoneis herculeana* (Ehrenberg) Cleve * +
    - *Gomphonema* group +
    - *Gyrosigma attenuatum* (Kuetzing) Cleve * +
    - *Melosira granulata* (Ehrenberg) Ralfs +
    - *Melosira varians* C. A. Agardh * +
    - *Navicula* group:
      - *N. dicephala* (Ehrenberg) Wm. Smith
      - *N. radiosa* Kuetzing +
      - *N. reinhardtii* (Grunow) Van Heurck+
      - *N. rhyncocephala* Kuetzing
    - *Nitzschia denticula* (Grunow) *
    - *Nitzschia palea* (Kuetzing) Wm. Smith*+
    - *Nitzschia sigmoidea* (Nitzsch) Wm. Smith *

*Organisms found on less than eight of the seventeen sampling days
+Refer to List of Plates in Table of Contents for location of photomicrograph of this organism.

TABLE VIII (Continued)

Nitzschia vermicularis
(Kuetzing) Hantzsch +
Pinnularia viridis
(Nitzsch) Ehrenberg * +
Rhizosolenia eriensis
H. L. Smith +
Rhoicosphenia curvata
(Kuetzing) Grunow * +
Stauroneis producta
Grunow *
Surirella group:
S. angusta
Kuetzing +
S. ovalis
Brebisson
S. ovalis
Brebisson var. *pinnata*
Wm. Smith +
Synedra acus
Kuetzing +
Synedra ulna
(Nitzsch) Ehrenberg+
Tabellaria fenestrata
(Lyngbye) Kuetzing +
Tabellaria flocculosa
(Roth) Kuetzing +

Class Chrysophyceae
Dinobryon sertularia

Phylum Chlorophyta

Ankistrodesmus falcatus
(Corda) Ralfs *
Cladophora glomerata
(Linnaeus) Kuetzing*
Closterium sp. *
Pediastrum duplex
Meyen *
Scenedesmus acuminatus
(Lagerheim) Chodat*
Scenedesmus quadricauda
(Turpin) Brebisson
Spirogyra sp. +
Tetraedron sp. *

Phylum Cyanophyta

Anabaena sp.
Lyngbya sp.
Merismopedia convoluta
Brebisson
Oscillatoria sp.
Raphidiopsis curvata
Fritsch *

The eight groups of organisms which were commonly found and whose average mean percentage composition at all depths was greater than one per cent were:

1. *Synedra acus*
2. *Achnanthes microcephala*
3. *Navicula* group
4. *Cymbella* group
5. *Gomphonema* group
6. *Cocconeis* group
7. Blue greens
8. Unidentified Diatoms

On the average these 8 groups comprised 93 per cent of the count at all depths. With the exception of the "blue-greens", which were not satisfactorily identified, all were diatoms. The blue-greens appeared to be a very small species of *Oscillatoria*. *Synedra acus* and *Achnanthes microcephala* were the outstanding organisms in each sample. For example, the average of the mean percentages at all depths for *Synedra acus* was 47.2 per cent, while a comparable figure for *Achnanthes microcephala* was 28.1 per cent. On the average, therefore, these two diatoms comprised seventy-five per cent of any one sample.

Synedra acus (Figure 6), reached its maximum of 2,523,000 per square centimeter at a depth of 2.5 feet on July 27. On the basis of mean counts, it can be seen that *Synedra acus*, in both absolute numbers and percentages of the total, decreased as the depth increased. In general, however, the counts at the twenty and thirty-five foot depths rose seasonally.

Achnanthes microcephala (Figure 5), the second most common organism of 1967, reached its maximum (1,002,000/cm.^{2}) on August 25 at a depth of twenty feet. As with *Synedra acus*, a marked variation according to depth occurred. In this case, however, the means of *Achnanthes microcephala* rose with increasing depth.

In comparing the per cent contribution to the total at each depth on each day for *Achnanthes microcephala* and *Synedra acus*, a balance was found between these two organisms. When the percentage of one was low, the other was high, and *vice versa*. In most instances, the combined percentage of these two diatoms was somewhere between seventy and eighty per cent.

In 1966, the genus *Achnanthes* was the predominant organism, with an average mean percentage contribution to the total of 32.1 per cent, while *Synedra* was second with a comparable figure of 26.4 per cent. Together, therefore, they averaged about fifty-nine per cent of the total. In 1967, on the other hand, these two diatoms comprised seventy-five percent of the total, with *Synedra acus* averaging 47.2 per cent of the total and *Achnanthes microcephala* 28.1 per cent. The changes that occurred in the individual order of predominance of these two and their combined contribution to the total in 1967 were probably due to several interrelated factors. The genus *Achnanthes* grows at the tips of gelatinous stalks which are attached to rocks by means of specialized holdfasts. *Synedra*, on the other hand, attached itself with a small amount of adhesive material secreted from one end of its frustule. These organisms are often found free-floating, while *Achnanthes* is rarely found unattached. The rough weather that had occurred during 1966, therefore, probably dislodged a proportionately greater number of *Synedra* than *Achnanthes* because of *Achnanthes*' superior mode of attachment. The counts reflected this in showing more *Achnanthes* than *Synedra*.

In 1967, calm weather prevailed and both organisms were subjected to optimal growth conditions. The results of 1967 show that *Synedra acus* "prefers" shallow water, for here the greatest numbers occurred. *Achnanthes*, in contrast, was proportionately more common in the deep water. Since bad weather in 1966 caused a great amount of turbulence in the shallow water, *Synedra* was adversely affected and, in that year, was exceeded in numbers by *Achnanthes*.

In 1967, the third most commonly occurring organism in the naturally occurring periphyton of Stony Point Bay was *Navicula*, with an average mean percentage of the total of 5.8 per cent. Two of the commonly occurring species are shown in Figures 10 and 11. The species included in this group are presented in Table VIII. In general, it was observed that *Navicula* increased with increasing depth. The maximum reached by this organism was 436,000 per square centimeter. In 1966, *Navicula* was the fifth most abundant organism and comprised, on the average, 6.1 per cent of the total at all depths.

The fourth most numerous organism in 1967 was *Cymbella* (group B, Table VIII). This group is made up of the smaller species of *Cymbella* and was most frequently represented by *Cymbella ventricosa* (Figure 8). The average mean percentage contribution to the total for all depths was 5.4 per cent. If all the species of *Cymbella* observed in 1967 had been grouped together, as they were in 1966, their average mean percentage contribution to the total would have been 6.0 per cent. In 1966, the genus *Cymbella* averaged 6.3 per cent of the total and was the fourth most common genus. In both 1966 and 1967, *Cymbella* decreased, in absolute numbers and percentage of the total, with increasing depth. The 1967 maximum for *Cymbella* group B was 262,000 per square centimeter.

Numberically, the fifth most common organism in 1967 was *Gomphonema* (Figures 14 and 15), which constituted an average of 2.5 per cent of the total at all depths. In 1966, this genus ranked seventh and averaged 2.6 per cent of the total. In the first year, no definite depth "preference" was noted for this organism, although the highest percentages occured at 2.5 and thirty-five feet. In 1967, the thirty-five foot counts were the highest, in both absolute numbers and percentage of the total.

The sixth most abundant organism for both years was Cocconeis (Figures 12 and 13). It averaged 3.7 per cent of the total for all depths in 1966 and 1.5 per cent in 1967. In both years, this organism was more common in the deeper water.

The last two groups, the unidentified blue green (probably Oscillatoria) and unidentifiable diatoms occupied the seventh and eighth positions in terms of abundance. The average mean percentage contribution to the to the total was 1.5 per cent for the blue-greens and 1.0 per cent for the diatoms.

The photomicrographs (Figures 16 through 40), show representative species of diatoms found as a part of the 1967 naturally occurring periphyton in Stony Point Bay. The photomicrograph of Rhizosolenia eriensis (Figure 35) is somewhat unusual, inasmuch as its delicate frustules usually do not survive the incineration process used in preparing permanent slides.

The dry and ash-free (organic) dry weights of all the 1967 Stony Point Bay samples are presented in Tables IX and X. The ash-free dry weights are shown graphically by Figures 48 through 53. Each weight is representative of a corresponding count, since samples for both determinations were taken from the same periphyton-water suspension. The dry weights (Table IX), in terms of mean weights for each depth, were highest at 2.5 feet and lowest at thirty-five feet. With the exception of the fifteen and twenty foot means, which were almost identical, the dry weights decreased with increasing depth. The mean ash-free dry weights (Table X) were highest at 2.5 feet and dropped regularly to their minimum at fifteen feet.

On the basis of the average of the 1967 mean dry weights for all depths, the total dry weight of the Stony Point Bay periphyton was calculated to be 55.5 tons (156 g./m.^{2}). The corresponding figure for the ash-free dry weights is 4.4 tons (12 g./m.^{2}) or 7.9 per cent of total dry weight.

When the means for the dry and ash-free dry weights are compared to the mean total counts for the six depths (Figure 4), it can be seen that both the dry and the ash-free dry weights, with one exception, vary with depth as do the mean counts. This apparent correlation between counts and weights is in distinct contrast to the situation observed in 1966. In that year, the relationship between the mean dry weights and the mean counts at the standard depths was inverse. When the counts rose, the weights dropped, and vice versa. The lack of correlation was attributed to the presence of sand in the samples. The 1967 data support this hypothesis, for in that year storm-caused turbulence was at a minimum and the mean ash-free and dry weights, in general, varied directly with the mean counts at each depth. The factors causing variations in the counts, therefore, can also be cited as causing variations in the weights. These factors were primarily the

TABLE IX

NATURALLY OCCURRING PERIPHYTON DRY WEIGHTS AT THE STANDARD SAMPLING DEPTHS, STONY POINT BAY, LAKE SUPERIOR, 1967. MILLIGRAMS PER SQUARE CENTIMETER OF ROCK SURFACE.

Date	Depth in Feet					
	2.5	5	10	15	20	35
7-11	28.8	7.4	9.0	7.8	3.3	6.0
7-13	30.0	8.7	4.4	6.2	9.2	7.9
7-17	19.7	26.1	9.6	6.1	7.4	--*
7-20	33.3	10.7	10.5	10.8	4.7	8.1
7-26	39.8	18.4	16.5	14.5	8.1	8.4
7-27	38.9	17.2	17.7	15.2	7.2	7.3
8-2	28.9	14.4	16.2	17.6	8.5	11.0
8-4	14.8	5.9	12.7	18.8	13.8	9.0
8-8	21.2	19.8	10.4	11.3	27.8	10.5
8-10	12.5	20.3	9.0	10.6	11.5	10.4
8-14	27.9	11.7	9.2	16.7	15.8	10.9
8-17	21.4	13.6	14.3	17.9	12.1	10.5
8-25	21.9	36.0	44.3	14.0	20.3	13.9
8-28	23.3	29.6	10.5	14.8	9.3	13.6
9-5	52.0	21.5	12.1	4.8	13.7	19.6
9-15	39.5	28.8	10.7	3.1	17.5	17.2
11-10	21.3	20.3	17.5	13.4	17.0	13.8
Mean	27.9	18.2	13.8	11.9	12.1	10.4

* Sample was lost

TABLE X

NATURALLY OCCURRING PERIPHYTON ASH-FREE DRY WEIGHTS AT THE STANDARD SAMPLING DEPTHS, STONY POINT BAY, LAKE SUPERIOR, 1967. MILLIGRAMS PER SQUARE CENTIMETER OF ROCK SURFACE.

	Depth in Feet					
Date	2.5	5	10	15	20	35
7-11	2.58	1.44	1.23	1.02	0.64	1.14
7-13	1.86	0.97	0.58	0.63	0.63	0.63
7-17	0.72	1.38	0.98	0.46	0.84	--*
7-20	1.95	1.26	1.03	0.85	0.47	0.69
7-26	3.43	2.64	2.00	1.22	1.05	1.07
7-27	1.99	1.60	1.38	1.11	0.30	0.96
8-2	1.66	1.50	2.07	1.29	0.97	1.09
8-4	0.85	0.70	1.12	1.22	0.97	1.04
8-8	1.71	1.88	1.19	1.10	1.97	1.58
8-10	0.68	1.36	0.71	0.55	0.72	0.80
8-14	1.15	0.88	0.52	0.93	1.08	0.82
8-17	1.46	1.02	1.01	0.77	0.72	1.61
8-25	1.39	1.92	2.25	1.01	1.66	1.18
8-28	1.90	2.35	1.38	1.81	1.04	1.48
9-5	3.48	2.37	1.50	0.88	1.82	2.32
9-15	1.90	1.82	0.81	0.33	1.25	1.65
11-10	0.33	0.73	0.85	0.44	0.55	1.17
Mean	1.70	1.51	1.21	0.91	0.98	1.20

* Sample was lost

weather, temperature and light intensity. The optimal weather conditions of 1967 probably explain why the total weight figure (55.5 tons or 156 g/m^2) for that year was higher than the 1966 figure (37.1 tons or 104 g/m^2).

In order to eliminate inconsistencies caused by the presence of sand, determinations of ash-free dry weights were made in 1967 even though this factor was minimal that year. If one consults Figures 42 through 47 and compares the findings with those presented in Figures 54 through 59, it will be seen that at each depth, the individual ash-free dry weights and the counts show an apparent positive correlation which extends over the entire sampling season.

To test this observation, regression lines were constructed using the least squares method. See figures 48 through 53. In constructing these figures counts were placed on the x axis and plotted against ash-free dry weights on the y axis. The correlation coefficients (r) and probability values (P) are presented with the regression lines. The correlation coefficients were positive for all depths, ranging from .492 at fifteen feet to .775 at ten feet. Probability values ranged from 0.05 at fifteen feet to 0.001 at ten and thirty-five feet. From these figures, it can be stated that to predict total counts from ash-free dry weights, one would be safest in choosing samples from ten and thirty-five feet. At these two depths, the correlations were the best and the probability values were lowest. The other depths also showed positive correlations between counts and weights, but were accompanied by slightly higher probability values.

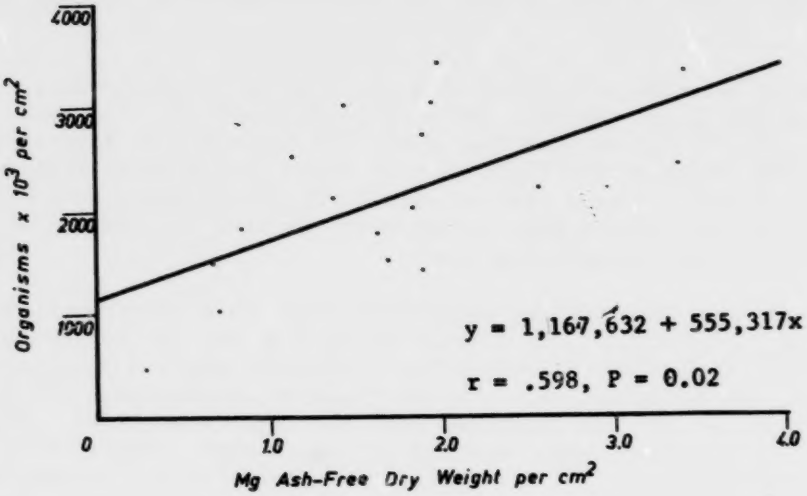

Figure 48. Counts versus ash-free dry weights, naturally occurring periphyton, 2.5 foot samples, Stony Point Bay, Lake Superior, 1967.

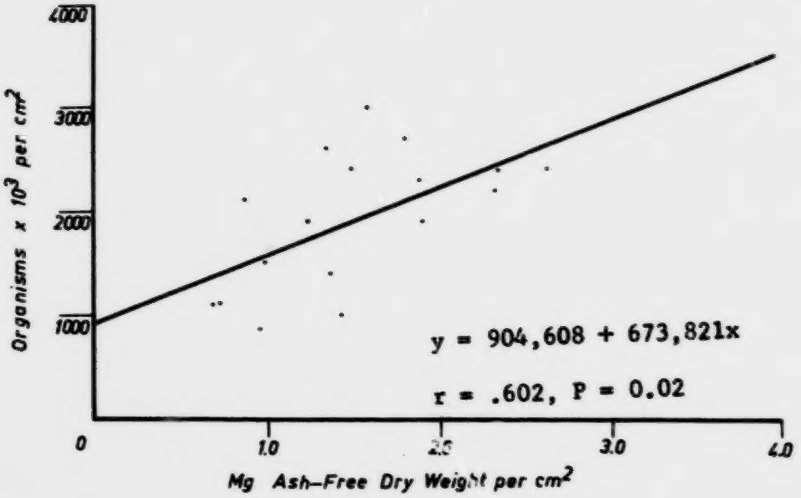

Figure 49. Counts versus ash-free dry weights, naturally occurring periphyton, five foot samples, Stony Point Bay, Lake Superior, 1967.

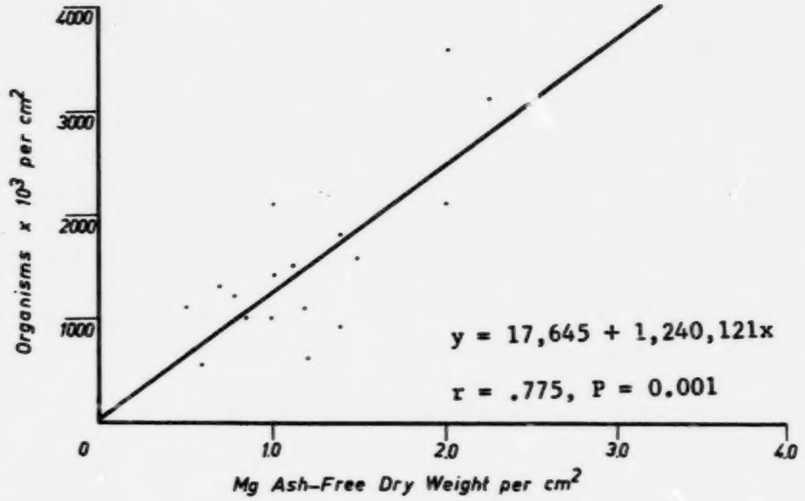

Figure 50. Counts versus ash-free dry weights, naturally occurring periphyton, ten foot samples, Stony Point Bay, Lake Superior, 1967.

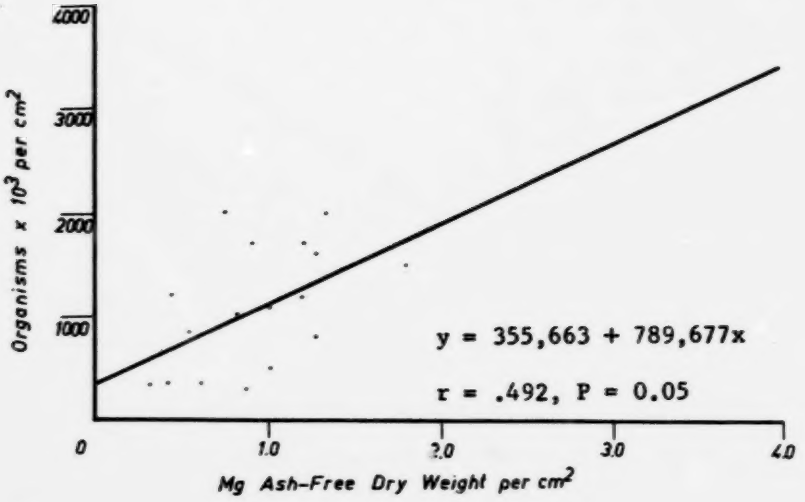

Figure 51. Counts versus ash-free dry weights, naturally occurring periphyton, fifteen foot samples, Stony Point Bay, Lake Superior, 1967.

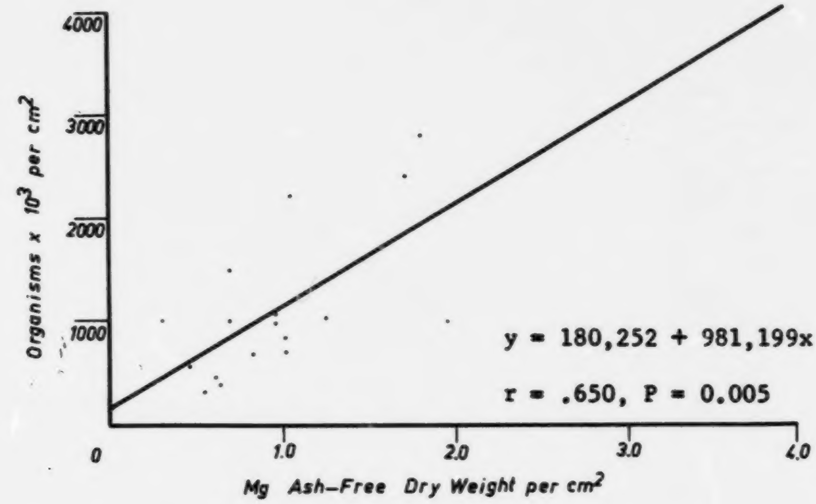

Figure 52. Counts versus ash-free dry weights, naturally occurring periphyton, twenty foot samples, Stony Point Bay, Lake Superior, 1967.

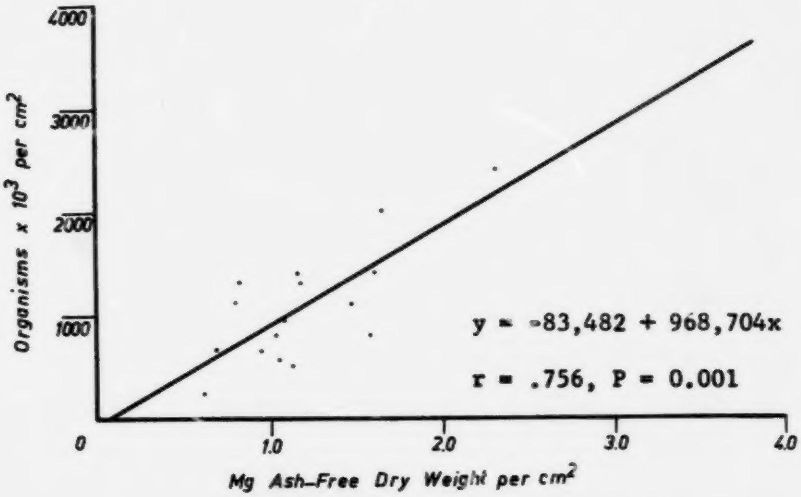

Figure 53. Counts versus ash-free dry weights, naturally occurring periphyton, thirty-five foot samples, Stony Point Bay, Lake Superior, 1967.

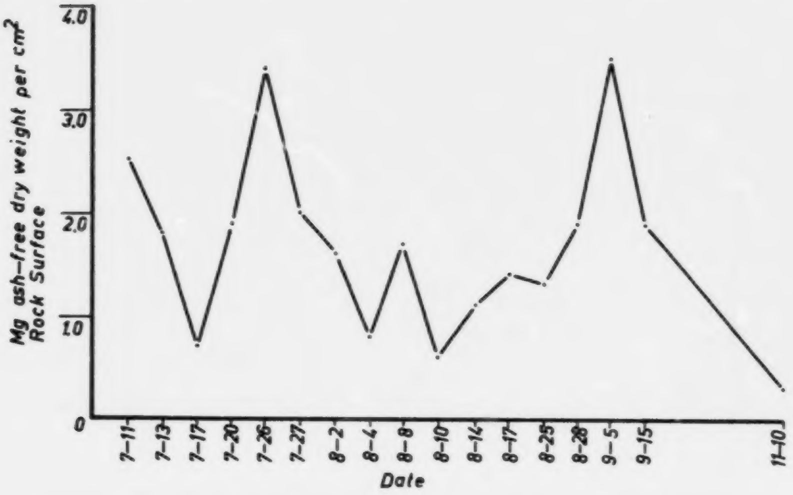

Figure 54. Naturally occurring periphyton ash-free dry weights at 2.5 feet, Stony Point Bay, Lake Superior, 1967.

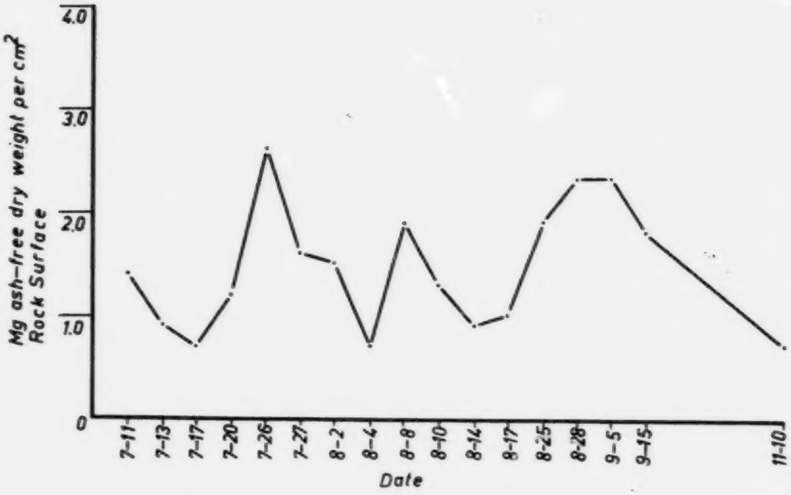

Figure 55. Naturally occurring periphyton ash-free dry weights at five feet, Stony Point Bay, Lake Superior, 1967.

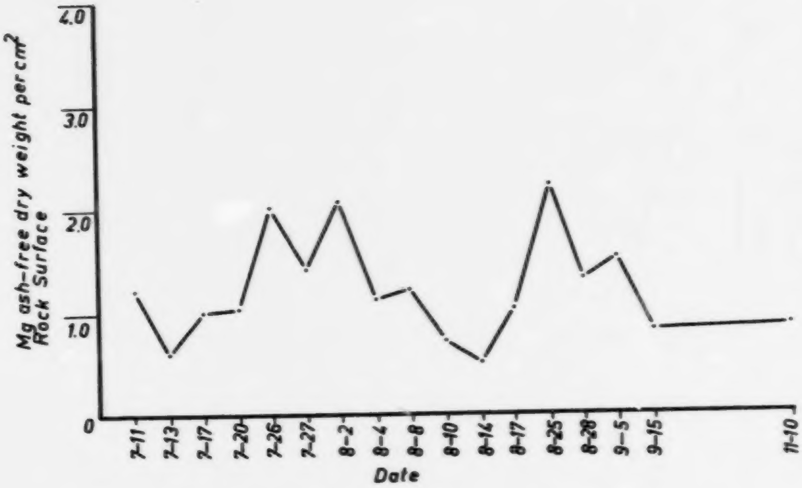

Figure 56. Naturally occurring periphyton ash-free dry weights at 10 feet, Stony Point Bay, Lake Superior, 1967.

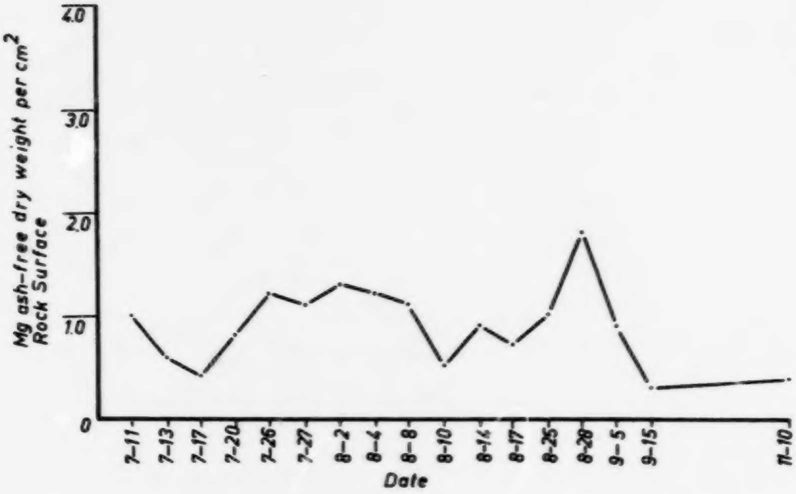

Figure 57. Naturally occurring periphyton ash-free dry weights at 15 feet, Stony Point Bay, Lake Superior, 1967.

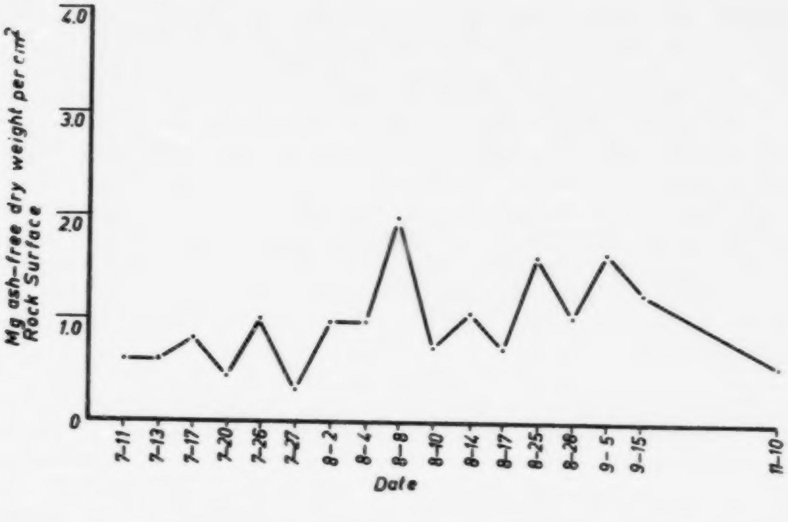

Figure 58. Naturally occurring periphyton ash-free dry weights at 20 feet, Stony Point Bay, Lake Superior, 1967.

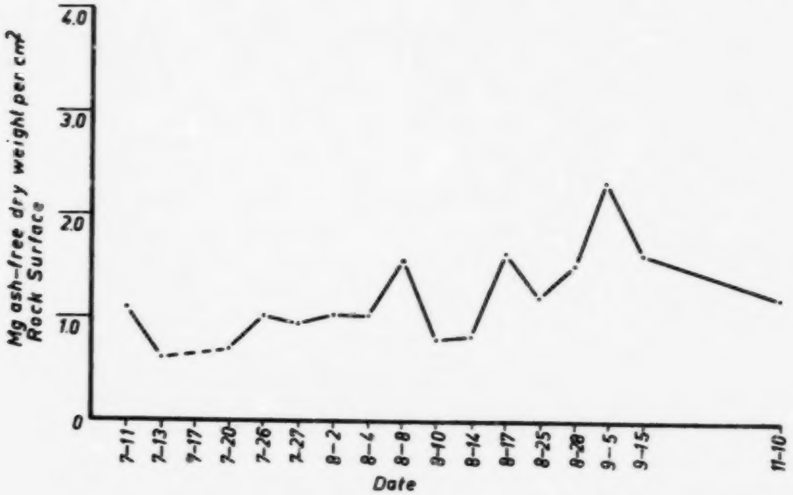

Figure 59. Naturally occurring periphyton ash-free dry weights at 35 feet, Stony Point Bay, Lake Superior, 1967.

Several times reference has been made to the fact that as the depth of the water increases in Lake Superior, the temperature drops and the amount of light reaching the bottom decreases. This is generally true even in the relatively shallow areas studied during this period of investigation. These assumptions relative to depth, temperature and light are substantiated by the findings presented in Table XI and Figure 60. Table XI, for example, shows the water temperatures of Stony Point Bay on all the collection days at each sampling depth (just above the bottom) as well as immediately below the surface. Two trends are obvious. The water temperatures decreased with increasing depth and increased at all depths as the summer progressed, reaching a maximum around August 14. For the whole season, the highest temperature (19.5°C.) was encountered by SCUBA divers at a depth of thirty-five feet on July 11, twenty and thirty-five feet on July 13, and thirty-five feet on November 10.

The light intensities reaching depths of water corresponding to the sampling depths are presented in Figure 60. Each point on the curve is an average of the light intensities in foot candles recorded at that particular depth on the seventeen sampling days. The average intensity of the sunlight striking the deck photometer was 7,275 foot candles. This figure was reduced to 5,600 foot candles by six inches of water. As expected, the intensity of the sunlight diminished gradually with depth, reaching a minimum of 265 foot candles at thirty-five feet. In general, readings were made near mid-day.

The hypothesis that decreased light intensity is responsible for the fact that the counts were lower in deeper water is supported by results reported by Ryther (1956b). In studying the effect of light on cultures of marine diatoms (Skeletonema costatum, Nitzschia closterium, and Navicula sp.), Ryther found that these organisms photosynthesized most effectively at light intensities of 1,000 to 2,200 foot candles. Below 1,000 foot candles, photosynthesis dropped rapidly. At 500 foot candles, for instance, a fifty per cent reduction occurred. From Figure 60, it can be seen that in Stony Point Bay at depths greater than about seventeen feet the light intensity is less than 1,000 foot candles. The minimum readings were taken at thirty-five feet and averaged 265 foot candles. At thirty-five feet, the total counts were, on the average, fifty per cent of the counts from 2.5 feet. Whether or not a reduction in photosynthesis is directly related to reduction of total counts was not determined. It seems logical to assume, however, that a reduction in photosynthesis would retard growth rate and, over a period of time, result in populations consisting of fewer organisms. In this study, Ryther also found that light intensities greater than 2,200 foot candles had an inhibitory effect on the photosynthesis of the diatoms. The deleterious effect of high light intensity on photosynthesis was less marked than the low intensity effect. At 5,000 foot candles, relative photosynthesis was reduced fifty per cent. The high counts of organisms from the shallow depths of Stony Point Bay, where light intensity was probably the greatest, do

TABLE XI

WATER TEMPERATURES AT THE SURFACE AND THE BOTTOM AT THE STANDARD SAMPLING DEPTHS, STONY POINT BAY, LAKE SUPERIOR, 1967. DEGREES CENTIGRADE.

	Depth in Feet						
Date	0.5	2.5	5	10	15	20	35
7-11	6.5	6.5	6.0	5.5	5.5	5.0	4.5
7-13	6.0	6.0	6.0	6.0	5.0	4.5	4.5
7-17	6.5	6.5	6.5	5.5	5.5	5.5	5.0
7-20	7.5	7.5	7.0	7.0	6.0	5.5	5.0
7-26	8.0	8.0	7.5	6.5	5.5	5.0	5.0
7-27	9.5	9.5	9.0	7.5	6.0	5.0	5.0
8-2	11.0	10.5	10.5	10.5	9.5	6.5	5.5
8-4	12.5	12.5	12.5	12.0	10.0	8.0	7.0
8-8	16.5	16.0	15.0	15.0	15.0	10.0	8.5
8-10	18.0	18.0	17.5	15.0	14.5	13.5	9.5
8-14	19.5	19.5	19.0	17.5	16.0	14.0	9.5
8-17	17.7	17.0	17.0	16.0	11.0	11.0	8.3
8-25	16.5	16.0	15.5	15.5	12.0	11.0	9.5
8-28	15.5	15.5	15.5	15.0	13.5	12.5	9.5
9-5	16.0	15.5	15.0	15.0	14.0	13.5	9.5
9-15	15.5	15.0	14.5	14.5	14.5	14.0	7.0
11-10	7.5	6.5	5.5	5.0	4.5	4.5	4.5

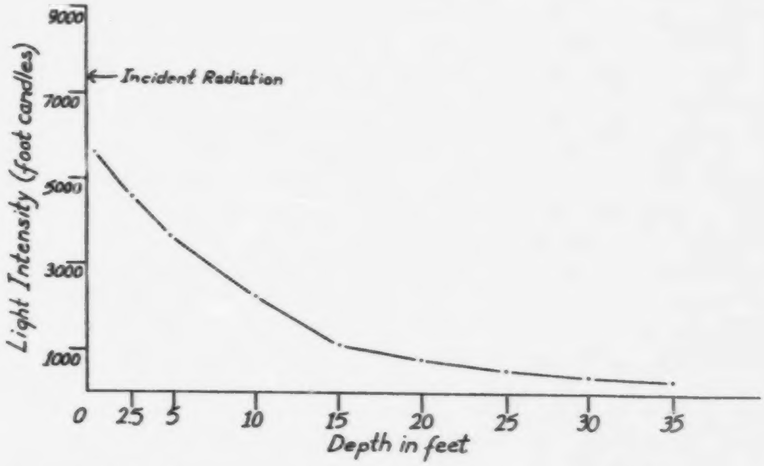

Figure 60. Average light intensity near mid-day, Stony Point Bay, Lake Superior, 1967.

not indicate that Lake Superior periphyton is inhibited by high light intensity. One explanation is that near shore, where the samples were taken, wave-caused turbidity probably filtered out harmful light.

The kinds and numbers of organisms found in the naturally occurring periphyton of oligotrophic waters have been determined only infrequently. Foerster and Schlicting (1965) studied the epiphytic periphyton growing upon leaves of rooted aquatic plants in an oligotrophic Texas lake. Their methods were similar to those used in this study. SCUBA diving procedures were employed to snip leaves from submerged plants. The leaf surfaces were washed free of periphyton and measured for area. Foerster and Schlicting found that most of the organisms growing on the leaves were diatoms, although five phyla of algae were represented. On the average, the counts obtained were from 300,000 to 500,000 organisms per square centimeter of leaf surface. These counts are comparable to those found for Lake Superior periphyton, especially those made in 1966, when a relatively lower growth level occurred. The diatoms found by Foerster and Schlicting included many genera observed in Lake Superior periphyton. Examples are Achnanthes, Synedra, Navicula, Nitzschia, Gomphonema, and Diatoma. The phyla they encountered were the three found in Lake Superior (Chrysophyta, Chlorophyta, and Cyanophyta), as well as Euglenophyta and Pyrrophyta.

Douglas (1958), in a quantitative study of naturally occurring periphyton, dealt with the periphyton of a stream in England. She concluded that her sampling apparatus was practical only for the collection of diatoms. Since this was a stream study, the organisms found could be expected to differ from those found in Lake Superior. This was not so, for the diatoms Douglas found were primarily Achnanthes, which usually varied in numbers from 100,000 to 500,000 per square centimeter of permanent rock surface. She recorded over a million per square centimeter several times. On stones in the stream, however, the maximum Achnanthes count was 270,000 per sqaure centimeter. The other commonly occurring genera were Synedra, Gomphonema, Cocconeis, Eunotia, Ceratoneis, and Cymbella. Douglas concluded that the substratum and the weather affect the number of organisms that occur. More diatoms were present on permanent rock than on stones. Rainstorms caused high water which scoured the substratum and removed the periphyton. The latter finding was also made by McIntire (1966), who observed that increased velocity adversely affects the periphyton growth in a laboratory stream. Lake Superior findings indicate that currents produced by storm winds scour the rocks, particularly in shallow water, and thereby reduce periphyton populations. Additional findings of Douglas showed that there did not seem to be a relationship between temperature or light intensity and growth of diatoms. In a shallow stream, however, light and temperature are not reduced by depth as they are in Lake Superior.

The general similarity between Douglas' findings and ours indicate that the periphyton environment in Lake Superior is not entirely unlike that of a stream. Moving masses of lake water constantly supply the attached growth with nutrients and flush away harmful metabolic by-products. The analogy is especially valid for the shallow water area of Lake Superior, for here the temperature and light intensity probably approach levels found in streams.

Duffer and Dorris (1966), like Douglas, concluded that the substratum affects the amount of periphyton growth that is produced. In studying the Blue River in Oklahoma, they found that "aufwuchs" productivity was higher on a granite stustratum than it was on limestone or sand. They concluded that a major factor in determining the magnitude of a stream's productivity is a favorable attachment surface for "aufwuchs". Genera of organisms found in Blue River periphyton included *Leptodictyon*, *Diatoma*, *Melosira*, *Synedra*, *Spirogyra*, *Rhizoclonium*, *Schizothrix*, and *Cladophora*. Duffer and Dorris also point out the fact that high productivity is not limited to organically enriched waters. The Blue River, Florida artesian springs, and Pacific coral reefs are examples of oligotrophic areas with high productivity.

The fact that the bodies of flowing water just discussed support genera of periphyton identical to Stony Point Bay genera emphasizes the ecological similarity between the bay and a stream. Furthermore, the findings of Douglas (1968) and Duffer and Dorris (1966) were not atypical. In her 1948 article, Ruth Patrick states that "in fast flowing streams only those forms which can attach themselves by gelatinous mass(es) or stalks can survive. Thus the typical genera of such habitats are *Achnanthes*, *Cocconeis*, *Cymbella*, and *Gomphonema*. *Ceratoneis arcus* is also considered a typical stream species." All of these organisms were found in Stony Point Bay periphyton, some in quite high numbers.

To classify a lake solely on the grounds of its algal components (either phytoplankton or periphyton) would be, at best, risky. The status of many of the so-called indicator species is uncertain. Rawson (1956), in a paper dealing with the phytoplankton of the Great Lakes and large oligotrophic lakes in western Canada, discusses several of these and questions species generally thought to be indicative of eutrophy. Patrick (1948), for instance, calls *Asterionella formosa* an indicator of eutrophic water while Rawson places the same species at the head of his list of indicators of oligotrophic waters. Often, the absence of certain groups of organisms may be as, or more, indicative of water quality than the presence of others. Thus, in Lake Superior, the fact that large numbers of Cyanophytes are not present is indicative of oligotrophy, for blue-greens grow best in water with a high nutrient content.

Many of the species of diatoms have a wide range of requirements and may occur under almost any conditions. Need (1953), for instance, found *Diatoma*, *Navicula*, *Gomphonema*, *Rhoicosphenia*, *Synedra*, and *Cymbella* in the periphyton of what he considered a polluted irrigation stream. All these forms are also present in Lake Superior periphyton. It might be added that Neel also found large numbers of blue-greens.

As long as it is realized that the presence or absence of particular species of organisms is the result of a great variety of physical, chemical and biological factors, biological indicators may be used to draw certain conclusions regarding a particular body of water. The validity of the conclusions depends a great deal on the number of physical and chemical factors known. The similarity between the abundant forms in Lake Superior periphyton and the forms present in oligotrophic streams and lakes suggests that the water of Stony Point Bay is relatively clean. Rawson (1956) lists species of the following genera as being indicators of oligotrophy: Asterionella, Tabellaria, Dinobryon, Fragilaria, Stephanodiscus, Staurastrum, and Melosira. In the oligotrophic lakes he studied, diatoms comprised eighty to ninety per cent of the phytoplankton populations. Rawson concludes by stating that only a few algal species can be used to indicate oligotrophy, whereas many species are limited to eutrophic waters. Thus, some organisms need, while others only prefer, high concentrations of nutrients. Very few, however, prefer low nutrient concentrations. This latter group would be indicators of oligotrophy. It is not surprising that there are so few of them. Although Rawson was discussing only phytoplankters, it seems logical to assume that his conclusions would also apply to organisms in the periphyton.

Regrowth of Periphyton

In 1967 studies on regrowth of periphyton on denuded rocks were carried out during the period of July 31 to November 9. In this time interval, eighty-four denuded, autoclaved rocks were replaced in the lake exposed for given period and then recovered for careful examination and quantitative measurements. The depths of exposure were ten, twenty and thirty-five feet. "Incubation" times ranged from eight hours to 101 days. The total counts at the time of each collection for all three depths is shown in Figure 61. In general, the counts increased with increased "incubation" times. Counts of samples from ten feet were higher than counts of twenty foot samples "incubated" for the same amount of time. Accordingly, the twenty foot counts were higher than the thirty-five foot counts. At ten feet, the counts reached 30,000 per square centimeter after forty-six days of "incubation". These ten foot counts always remained higher than counts of samples from the other two depths "incubated" for the same period of time. In the same forty-six day time interval, the twenty foot counts went from 16,000 per square centimeter to 340,600 per sqaure centimeter. The thirty-five foot samples ranged from 8,000 organisms per square centimeter after eight hours of "incubation" to 215,500 per square centimeter after forty-six days. By November 9, the count had dropped to 129,200 per square centimeter. In general, the counts rose fairly regularly with time at all depths.

A checklist of the organisms occurring as regrowth is given in Table XII. A total of at least forty-seven species representing thirty genera and three phyla were found. Forty of the species (eighty-five per cent) and twenty-three of the genera (seventy-seven per cent)

TABLE XII

ORGANISMS OCCURRING AS REGROWTH ON ARTIFICIALLY DENUDED ROCKS, STONY POINT BAY, LAKE SUPERIOR, 1967.

Phylum Chrysophyta

Class Bacillariophyceae
- *Achnanthes microcephala*
  (Kuetzing) Cleve
- *Amphora ovalis*
  Kuetzing
- *Amphora normani*
  Rabenhorst
- *Asterionella formosa*
  Hassall
- *Ceratoneis arcus*
  (Ehrenberg) Kuetzing
- *Cocconeis* group*
- *Cyclotella* group*
- *Cymatopleura solea*
  (Brebisson) Wm. Smith
- *Cymbella* group A*
- *Cymbella* group B*
- *Denticula thermalis*
  Kuetzing
- *Diatoma elongatum*
  C.A. Agardh var. *tenuis*
  (Agardh) Van Heurck
- *Fragilaria capucina*
  Desmazieres
- *Fragilaria harrisonii*
  (Sm. Smith) Grunow
- *Frustulia viridula*
  (Brebisson) DeToni
- *Gomphoneis herculeana*
  (Ehrenberg) Cleve
- *Gomphonema* group
- *Melosira granulata*
  (Ehrenberg) Ralfs
- *Navicula* group*
- *Nitzschia palea*
  (Kuetzing) Wm. Smith
- *Nitzschia vermicularis*
  (Kuetzing) Hantzsch
- *Pinnularia viridis*
  (Nitzsch) Ehrenberg
- *Rhizosolenia eriensis*
  H. L. Smith
- *Stauroneis producta*
  Grunow
- *Surirella* group*
- *Synedra acus*
  Kuetzing
- *Synedra ulna*
  (Nitzsch)Ehrenberg
- *Tabellaria fenestrata*
  (Lyngbye) Kuetzing
- *Tabellaria flocculosa*
  (Roth) Kuetzing

Class Chrysophyceae
- *Dinobryon sertularia*
  Ehrenberg

Phylum Chlorophyta

- *Cosmarium* sp.
- *Scenedesmus quadricauda*
  (Turpin) Brebisson

Phylum Cyanophyta

- *Anabaena* sp.
- *Lyngbya* sp.
- *Merismopedia convoluta*
  Brebisson
- *Oscillatoria* sp.

* See Table VIII for the species comprising this group.

were diatoms. *Dinobryon sertularia* was the only "non diatom" Chrysophyte observed. Two species of greens and four species of blue-greens were found.

The numbers of organisms in each of the three phyla, as well as the total counts of all the regrowth samples, are shown in Table XIII. No averages are presented, for they would be meaningless in this type of study. In all but one of the samples, the phylum Chrysophyta comprised over ninety per cent of the total number of organisms. The vast majority of the Chrysophytes were diatoms. *Dinobryon sertularia* was present in low numbers and appeared only near the end of the sampling season. Since most of the organisms were diatoms, their variation may be seen graphically in Figure 61, which shows the total counts for each depth versus "incubation" time.

By looking at Table XIII, it can be seen that the greens and blue-greens do show a rising trend with increased "incubation" times. Because of the fact that they occurred in such small numbers, however, any conclusions that might be drawn by looking at these figures would be highly speculative. It can only be pointed out that greens and blue-greens did appear as regrowth, but in relatively low numbers.

In these regrowth studies the two predominant organisms were *Synedra acus* and *Achnanthes microcephala*. Together, these two diatoms comprised an average of sixty-eight per cent of the total counts at all three depths. In terms of percentage contribution to the total, *Achnanthes microcephala* climbed regularly at all depths with increasing "incubation" time, as did *Synedra acus*. For the whole study, *Synedra acus* was predominant. Among the initial colonizers, on the other hand, *Achnanthes microcephala* was the predominant form. In terms of percentage of the total, *Achnanthes microcephala*, with one exception, was higher than *Synedra acus* after eight and forty-eight hours of "incubation" at all depths. The exception was at ten feet after eight hours. Graphically, the order of predominance (in absolute numbers and percentage contribution to the total) of *Achnanthes microcephala* (A) and *Synedra acus* (S) according to incubation time and depth may be presented as follows:

	8 hrs.	48 hrs.	96 hrs.	8 days	14-46 days
10 feet	S	A	S	S	S
20 feet	A	A	S	S	S
35 feet	A	A	A	A	S

The fact that *Achnanthes microcephala* was the initial colonizer supports the conclusion that one of the reasons *Achnanthes* was predominant in 1966 (when much rough weather occurred) was its superior mode of attachment.

The two other primary colonizers at all depths in the 1967 regrowth study appeared to be *Navicula* spp. and *Gomphonema* spp. Fairly substantial numbers of *Cymbella* spp. (group B) appeared early at ten feet. After a week of regrowth, *Asterionella formosa*, *Cocconeis* spp., *Cyclotella* spp., *Cymbella* spp. (group B), *Melosira granulata* and the unidentified blue-greens appeared regularly at all depths.

TABLE XIII

PHYLA AND COUNTS OF ORGANISMS OBSERVED IN REGROWTH PERIPHYTON, STONY POINT BAY, LAKE SUPERIOR 1967. ORGANISMS X 10^3 PER SQUARE CENTIMETER OF ROCK SURFACE.

Depth in Feet	Phylum	*Date and "Incubation Time" Jul 31 8 hrs	Aug 2 48 hrs	Aug 4 96 hrs	Aug 8 8 days	Aug 14 14 days	Aug 25 25 days	Aug 28 28 days	Sep 5 36 days	Sep 15 46 days	Nov 9 101 days
	Chrysophyta	28.8	76.0	55.7	184.7	212.5	345.7	278.1	338.7	368.3	
10	Chlorophyta	0.5	1.0	4.5	2.7	3.7	5.9	0.9	5.1	---	N.S.
	Cyanophyta	1.0	3.0	---	---	12.3	5.9	5.5	7.7	2.2	
	TOTAL:	30.3	80.0	60.2	187.4	228.5	357.5	284.5	351.5	370.5	
	Chrysophyta	16.1	60.1	21.4	57.0	146.9	190.8	177.1	193.4	314.2	
20	Chlorophyta	---	---	---	3.4	5.3	3.9	0.7	0.6	1.8	N.S.
	Cyanophyta	---	0.7	1.6	---	8.4	9.6	4.8	20.5	24.6	
	TOTAL:	16.1	60.8	23.0	60.4	160.6	204.3	182.6	214.5	340.6	
	Chrysophyta	8.0	25.3	38.4	8.4	66.0	173.6	102.2	149.9	208.3	123.9
35	Chlorophyta	---	---	1.1	1.4	---	3.3	4.2	1.0	2.4	---
	Cyanophyta	---	---	---	---	---	5.5	3.4	6.9	4.8	5.3
	TOTAL:	8.0	25.3	39.5	9.8	66.0	182.4	109.8	157.8	215.5	129.2

*Dash indicates zero; N.S. indicates no sample was collected.

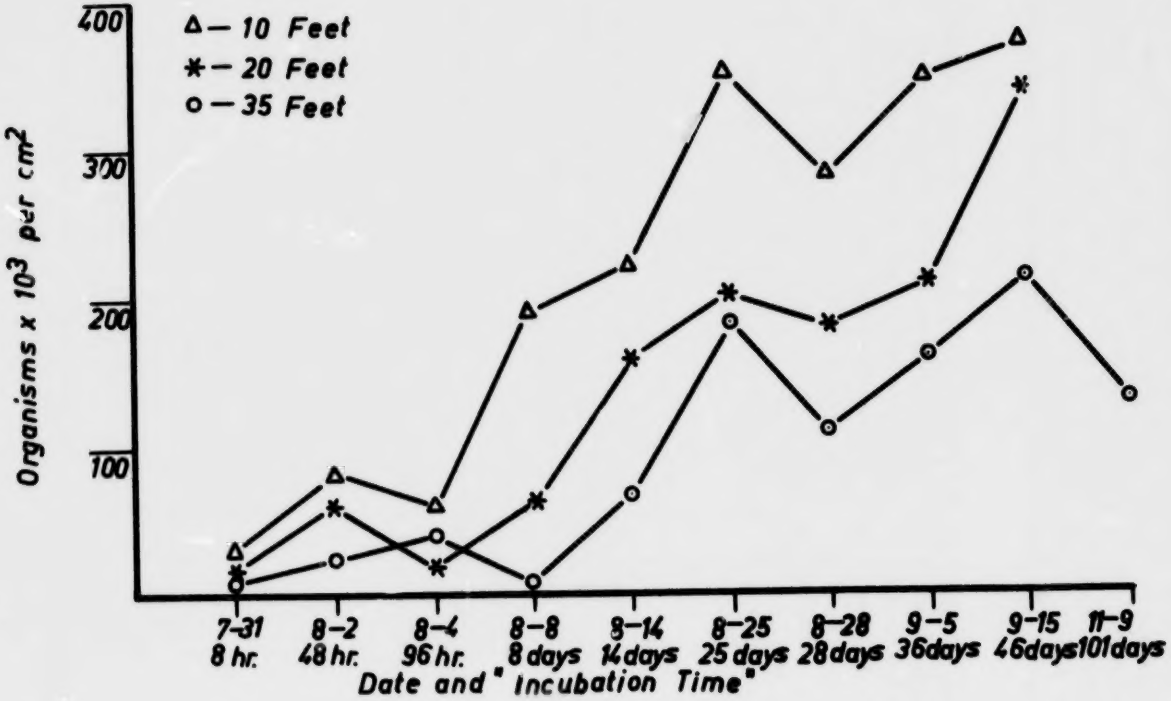

Figure 61. Total counts of periphyton appearing as regrowth, Stony Point Bay, Lake Superior, 1967.

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The dry and the ash-free dry weights of the regrowth periphyton are shown in Table XIV. In general, the weights increased with prolonged "incubation" time and decreased with depth. Since the weights of two groups of samples collected after different "incubation" times are not comparable, means for these weights are not presented. When the weights obtained on the last regular day of sampling (September 15) are divided by their "incubation" time (forty-six days), a daily production rate can be calculated. For the dry weights at ten, twenty, and thirty-five feet the rates are 5.76, 2.26, and 2.77 grams per square meter per day. On the basis of the ash-free dry weights, comparable figures for the three depths are 0.09, 0.05, and 0.06 grams per square meter per day.

Figures 62 through 64 show the regression lines obtained when one attempts to predict total counts from ash-free dry weights. Correlation coefficients and probability values are presented with the regression lines. The best correlation coefficient (.803) and the lowest probability value (0.01) were obtained with the data from ten feet. Although the correlation coefficients for the twenty and thirty-five foot data (.574 and .605) were not exceedingly low, their corresponding probability values were quite high (0.1 for both) because of the low number of samples.

TABLE XIV

DRY AND ASH-FREE DRY WEIGHTS OF PERIPHYTON
OCCURRING AS REGROWTH, STONY POINT BAY, LAKE SUPERIOR, 1967.
MILLIGRAMS PER SQUARE CENTIMETER OF ROCK SURFACE.

	Dry Weight Depth in Feet				Ash-Free Dry Weight Depth in Feet		
Date	10	20	35	Date	10	20	35
7-31	.68	.28	.62	7-31	.06	.02	.04
8-2	.54	.27	.30	8-2	.17	.01	.09
8-4	1.65	.80	.59	8-4	.23	.18	.17
8-8	1.92	1.83	.78	8-8	.45	.18	.13
8-14	5.03	6.96	5.36	8-14	.64	.57	.54
8-25	13.8	7.49	12.82	8-25	1.21	.52	.77
8-28	16.53	11.71	6.10	8-28	.49	.37	.26
9-5	7.97	9.48	4.22	9-5	1.03	.40	.75
9-15	26.49	10.41	12.75	9-15	.43	.24	.29
11-9	N.S.*	N.S.	7.02	11-9	N.S.	N.S.	.13

* N.S. means no sample was collected.

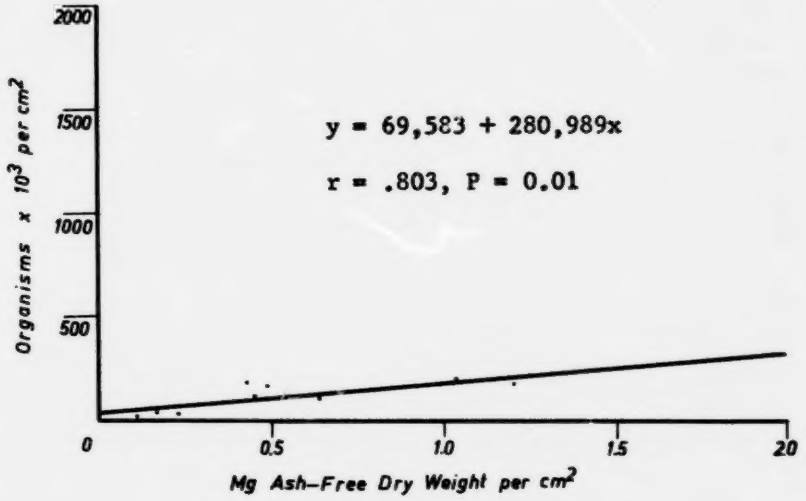

Figure 62. Counts versus ash-free dry weights, regrowth study, ten foot samples, Stony Point Bay, Lake Superior, 1967.

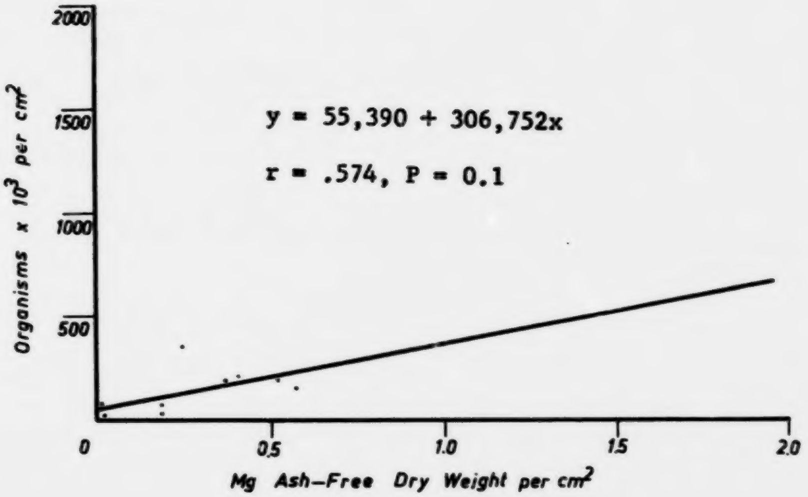

Figure 63. Counts versus ash-free dry weights, regrowth study, twenty foot samples, Stony Point Bay, Lake Superior, 1967.

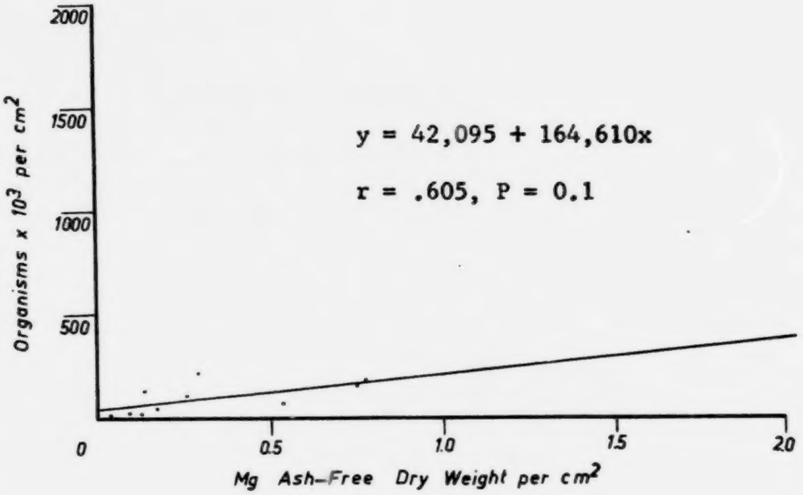

Figure 64. Counts versus ash-free dry weights, regrowth study, thirty-five foot samples, Stony Point Bay, Lake Superior, 1967.

Since only qualitative regrowth data was obtained during 1965, quantitative comparisons to the 1967 data cannot be made. The organisms in the checklists for these two summers, however, are comparable. In 1965 (Table II), thirty-four genera of Chrysophytes, Chlorophytes, and Cyanophytes were found. In 1967, the same three phyla were represented by thirty genera. Genera observed in 1965 and not seen in the 1967 regrowth samples were: Chrysophytes - Diploneis, Rhoicosphenia, and Stephanodiscus; Chlorophytes - Actinastrum, Closterium, Coelastrum, Oedogonium and Tetraedron. The four genera observed in the 1967 counts and not seen in 1965 included one diatom, Gomphoneis, and three blue-greens: Anabaena, Lyngbya, and Oscillatoria. With these exceptions, the genera on both checklists were seen both summers. From this comparison, it can be seen that the organisms in the regrowth for 1965 and 1967 were quite similar, at least qualitatively.

In order to see how close the 1967 regrowth approximated the naturally occurring growth, the following comparison was made. The regrowth counts reached their maximum at all depths after forty-six days of "incubation". If the September 15 regrowth counts are compared to the 1967 naturally occurring counts for the same date, it will be seen that the regrowth level reached was approximately fourteen per cent of the naturally occurring growth level at ten feet, twenty-eight per cent at twenty feet, and eleven per cent at thirty-five feet. From this comparison, it is clear that the quantity of regrowth that occurs after forty-six days of "incubation" is far below the amount of naturally occurring periphyton.

In the forty-six day growth period, thirty genera of algae appeared on the rocks. In contrast, thirty-eight genera were found in the naturally occurring periphyton in 1967. The only genus that appeared as regrowth and was not seen in the naturally occurring periphyton was *Cosmarium*, which appeared in very low numbers and in one sample only. Genera of naturally occurring periphyton that did not appear in the regrowth in 1967 were: Chrysophyta - *Gyrosigma* and *Rhoicosphenia*; Chlorophyta - *Ankistrodesmus*, *Cladophora*, *Closterium*, *Pediastrum*, *Spirogyra*, and *Tetraedron*; Cyanophyta - *Raphidiopsis*. All of these genera, most of which are greens, appeared in relatively low numbers. The fact that they did not appear as regrowth is probably not significant. The most common genera in the naturally occurring periphyton of 1967 were also the most numerous regrowth forms. On the basis of the means of the September 15 counts from the three depths for each organism, the most abundant forms in the regrowth, in order, were *Synedra acus*, *Achnanthes microcephala*, *Navicula* spp., *Cymbella* spp. (group B), and *Gomphonema* spp. These werealso the five most commonly occurring organisms in the 1967 naturally occurring periphyton. Even the order of abundance was almost identical. In the naturally occurring periphyton, *Gomphonema* spp. was more common than *Cymbella* spp. (group B). The naturally occurring periphyton populations and those occurring as regrowth both showed a preponderance of diatoms in all samples; low numbers of greens and blue-greens showed no marked trends, either seasonally or according to depth, and a decrease in counts with increasing water depth. The primary difference between the two communities was one of quantity.

Most of the past studies encountered in the literature have dealt with periphyton occurring as regrowth on some artificial substratum. Gumtow (1955) was one of the few workers who used a natural substratum in studying periphyton regrowth. He cleaned cobblestones taken from the bank of the West Gallatin River in Montana by rinsing them in formalin. After placing them in the river for varying periods of time, he found that the most common genera of diatoms appearing as regrowth were *Navicula*, *Diatoma*, *Cymbella*, *Cocconeis*, *Synedra*, and *Ceratoneis*.

Plexiglas and glass have been the most common materials used as artificial substrata. Jackson (1967) used plexiglas plates in studying the periphyton of the eastern end of Lake Ontario. He identified the organisms occurring as regrowth to genus and estimated their abundance. He also determined their monthly biomass in terms of organic weight per square decimeter of plate surface. The most common organisms found were diatoms. Of the seventeen genera recorded, *Melosira* and *Stephanodiscus* were always common. The most abundant of the ten genera of greens observed was *Cladophora*, an organism which has created nuisance problems in Lakes Erie and Ontario since the early nineteen-thirties (Neil and Owen, 1964). None of the five genera of Cyanophytes were considered abundant by Jackson. All of the diatom genera reported were also observed in Lake Superior periphyton.

Kevern *et al*. (1966) and King and Ball (1966) also used plexiglas plates as a substratum for regrowth. Kevern et al. used this method to determine the periphyton production in a laboratory stream. Their average estimate for daily net production was 0.6 grams of organic (ash-free dry) weight per square meter per day. King and Ball arrived at a comparable figure of about 0.3 grams per square meter per day. In their study of the Red Cedar River in Michigan, they found that almost all the organisms occurring as regrowth were diatoms. The most common genera were Gomphonema, Navicula, Fragilaria, Cymbella, Cyclotella, and Synedra.

Castenholz (1960) used glass slides as a substratum in studying the periphyton of lakes in the state of Washington. Common diatoms appearing as regrowth were Achnanthes, Amphora, Cocconeis, Cymbella, Gomphonema, Navicula, Nitzschia, and Stephanodiscus. A typical high production rate was 0.5 grams per square meter per day of organic weight. Castenholz felt that glass was not unduly selective and that a two week period of submergence was sufficient for determining production rates. Foerster and Schlicting (1965), on the other hand, came to a different conclusion. After comparing the natural periphyton growth in a Texas lake to regrowth on glass slides, they stated that "the artificial barren surface gave a false impression of the productivity trends and indicated only some of the significant genera present in the ecosystem."

In looking at these regrowth results from other bodies of water, most of which were streams, it can be seen that the genera of organisms found are remarkably similar to those found in Lake Superior periphyton. The production figures, however, are a good deal higher than those found for Lake Superior periphyton. The average daily production rate for the three depths sampled in Stony Point Bay was 0.066 grams per square meter while others reported figures from streams of as high as 0.6 grams per square meter per day. Whether or not regrowth on glass or other artificial substrata is comparable to regrowth on a natural substratum is debatable, as has been shown. It must also be remembered that the Lake Superior regrowth study was conducted at depths of ten, twenty, and thirty-five feet. Had regrowth production rates been determined for the very shallow water area of Stony Point Bay, figures comparable to those reported for streams may have resulted.

Naturally Occurring North Shore Periphyton

This study included eleven sampling areas along the North Shore of Lake Superior extending approximately 107 miles from the zero station at Lester River. The points involved are listed in the tabulation given below.

PERIPHYTON SAMPLING LOCATIONS,
NORTH SHORE, LAKE SUPERIOR.

1. Lester River	0 miles
2. Knife River	13.8 miles
3. Burlington Bay	22.1 miles

Periphyton Sampling Locations (Cont'd)

4.	Split Rock River Bay	39.4 miles
5.	Beaver Bay	48.0 miles
6.	No-Name Bay (near Little Marais)	53.9 miles
7.	Sugar Loaf Cove	69.9 miles
8.	Tofte	78.8 miles
9.	Lutsen	86.3 miles
10.	Good Harbor Bay	100.9 miles
11.	Grand Marais	106.9 miles

The geographic locations of each of these sampling points can be obtained by reference to the accompanying map (Figure 3).

The results of the North Shore study has been summarized in Tables XV, XVI, XVII, and XVIII. Table XV for example deals with organisms found and their abundance and mean weights. In preparing the latter table, counts from all depths on the two sampling days for each station were averaged to give the mean total count. This figure was rounded off to the nearest ten thousand organisms per square centimeter of rock surface. The individual total counts for all depths on the two sampling days for each north shore station are shown in Figures 65 through 75. In Table XV, the dry and ash-free dry weights, expressed as milligrams per square centimeter of rock surface, are also expressed as means. Individual weights are shown in Table XVI.

The five most common organisms in Table XV were calculated on the basis of their total numbers per square centimeter of rock surface at a particular station, regardless of depth or day collected. They are presented in their order of abundance.

The water temperatures recorded while sampling the north shore stations are shown in Table XVII.

The 1967 total counts, with only a few exceptions, were higher at the north shore stations than were counts for the same year at Stony Point Bay (1,470,000 per square centimeter). The exceptions were samples from the Lester River area, the Knife River area, and Sugar Loaf Cove. These stations were similar to Stony Point Bay.

The lowest mean count (1,466,000/cm.^{2}) was recorded at Sugar Loaf Cove. This area has been and still is the site of a large logging operation. At times, the entire cove was filled with floating logs, which undoubtedly diminished the sunlight reaching the bottom. Also, large amounts of wood chips were noted covering the rocks, again, causing a reduction in available sunlight.

Counts of over three million organisms per square centimeter were recorded at Split Rock River Bay, Good Harbor Bay, and Grand Marais. Only the Grand Marais sampling area was near a relatively large popula-

TABLE XV
SUMMARY OF RESULTS, NORTH SHORE STATIONS, LAKE SUPERIOR, 1967

Study Area	Mean Total Count*	Mean Weights**		Five Most Common Organisms
		Dry	Ash-Free	
Lester River	1,693,000	19.5	1.46	*Achnanthes microcephala*, *Synedra acus*, *Cymbella* spp., *Navicula* spp., *Nitzschia* spp.
Knife River	1,526,000	9.5	1.16	*S. acus*, *A. microcephala*, *Navicula* spp., *Cymbella* spp., unidentified blue-green
Burlington Bay	2,890,000	16.6	1.50	*S. acus*, *A. microcephala*, *Navicula* spp., unidentified blue-green, *Cymbella* spp.
Split Rock River Bay	3,798,000	12.5	1.35	*S. acus*, *A. microcephala*, *Cymbella* spp., *Navicula* spp., *Synedra ulna*
Beaver Bay	2,964,000	31.5	2.31	*S. acus*, *A. microcephala*, *Cymbella* spp., *Navicula* spp., *Gomphonema* spp.
No-Name Bay	2,294,000	5.65	0.84	*S. acus*, *A. microcephala*, *Navicula* spp., *Cymbella* spp., *Gomphonema* spp.
Sugar Loaf Cove	1,466,000	2.72	0.61	*A. microcephala*, *S. acus*, *Cymbella* spp., *Navicula* spp., *Gomphonema* spp.
Tofte	2.291,000	5.5	0.97	*S. acus*, *A. microcephala*, *Cymbella* spp., *Navicula* spp., *Gomphonema* spp.
Lutsen	2,497,000	9.5	0.89	*S. acus*, *A. microcephala*, *Cymbella* spp., *Navicula* spp., unidentified blue -green
Good Harbor Bay	3,020,000	10.5	1.51	*S. acus*, *A. microcephala*, *Cymbella* spp., *Navicula* spp., *Synedra ulna*
Grand Marais	3,309,000	16.0	1.60	*S. acus*, *A. microcephala*, *Cymbella* spp., *Navicula* spp., *Ceratoneis arcus*

* Organisms per square centimeter of rock surface

** Milligrams per square centimeter of rock surface

TABLE XVI

PERIPHYTON DRY WEIGHTS AT SEVERAL DEPTHS, NORTH SHORE STATIONS, LAKE SUPERIOR, 1967. MILLIGRAMS PER SQUARE CENTIMETER OF ROCK SURFACE.

			Depth in Feet			
Date	2.5	5	10	15	20	35
			Lester River			
8-16	2.9	10.1	47.5	76.5	13.9	---
9-6	2.6	5.0	5.4	11.6	13.9	---
			Knife River			
9-5	2.8	5.0	3.6	4.3	6.8	36.3
9-15	1.1	1.1	3.5	3.2	35.8	9.8
			Burlington Bay			
8-22	7.7	3.7	13.9	20.5	---	---
9-1	17.8	9.5	35.2	19.6	22.0	---
			Split Rock River Bay			
8-29	4.8	7.6	7.6	22.6	25.1	---
9-7	7.7	9.6	13.8	9.7	14.4	14.9
			Beaver Bay			
8-29	4.5	11.0	9.4	13.1	49.8	42.8
9-14	15.1	29.9	45.4	56.4	51.8	48.6
			No-Name Bay			
9-1	4.5	2.8	13.2	3.2	4.1	---
9-14	3.6	3.3	12.6	5.7	3.5	---
			Sugar Loaf Cove			
8-31	2.0	1.9	1.7	1.5	5.5	---
9-7	3.5	1.9	4.5	2.4	2.3	---
			Tofte			
8-31	2.7	4.3	3.6	3.9	2.6	8.4
9-7	4.1	3.7	4.9	10.5	2.6	14.4
			Lutsen			
8-31	9.5	7.5	6.2	8.0	11.3	10.6
9-7	8.9	13.5	8.4	7.5	2.5	9.6
			Good Harbor Bay			
8-31	4.0	9.1	6.1	17.5	16.7	15.4
9-7	8.4	9.1	6.2	19.4	11.1	2.8
			Grand Marais			
8-31	4.9	19.3	12.9	22.2	28.6	5.8
9-7	2.1	21.7	21.1	21.9	24.7	7.8

TABLE XVII

PERIPHYTON ASH-FREE DRY WEIGHTS AT SEVERAL DEPTHS, NORTH SHORE STATIONS, LAKE SUPERIOR, 1967. MILLIGRAMS PER SQUARE CENTIMETER OF ROCK SURFACE.

Date	Depth in Feet 2.5	5	10	15	20	35
Lester River						
8-16	0.38	1.23	3.33	3.54	---	---
9-6	0.90	1.25	0.63	0.91	0.95	---
Knife River						
9-5	0.34	0.70	0.73	0.66	0.90	3.84
9-15	0.23	0.42	0.59	0.31	2.81	2.40
Burlington Bay						
8-22	1.03	0.63	1.47	1.95	---	---
9-1	1.39	0.98	2.45	1.54	2.07	---
Split Rock River Bay						
8-29	0.55	0.81	1.04	1.02	2.04	---
9-7	0.57	0.87	2.13	1.64	2.27	1.88
Beaver Bay						
8-29	0.50	0.82	0.72	2.32	4.25	2.80
9-14	0.84	2.62	4.07	3.75	3.55	3.58
No-Name Bay						
9-1	0.76	0.46	1.75	0.56	0.60	---
9-14	0.59	0.42	1.75	0.80	0.69	---
Sugar Loaf Cove						
8-31	0.27	0.14	0.42	0.60	0.94	---
9-7	0.29	0.41	1.04	1.17	0.79	---
Tofte						
8-31	0.43	0.72	0.66	0.89	0.57	1.24
9-7	0.76	0.82	1.14	1.80	0.50	1.95
Lutsen						
8-31	0.49	0.49	0.27	0.65	1.22	0.91
9-7	1.43	1.89	0.97	1.14	0.39	1.13
Good Harbor Bay						
8-31	0.53	0.97	1.16	2.44	2.67	1.32
9-7	0.81	0.98	0.67	3.21	1.85	0.59
Grand Marais						
8-31	0.65	1.61	2.09	3.74	0.91	0.55
9-7	0.31	1.90	1.76	2.73	2.50	0.57

TABLE XVIII

WATER TEMPERATURES AT THE SURFACE AND THE BOTTOM AT THE STANDARD SAMPLING DEPTHS, NORTH SHORE STATIONS, LAKE SUPERIOR, 1967. DEGREES CENTIGRADE.

	Depth in Feet						
Date	0.5	2.5	5	10	15	20	35
Lester River							
8-16	21.5	21.5	20.0	9.0	8.0	---	---
9-6	23.0	22.5	21.0	20.0	11.0	9.0	---
Knife River							
9-5	15.0	15.0	14.5	14.0	11.0	6.0	6.0
9-15	15.5	15.5	14.5	14.0	8.0	7.5	7.0
Burlington Bay							
8-22	13.0	13.0	12.5	12.0	10.0	---	---
9-1	13.0	13.0	13.0	13.0	13.0	13.0	---
Split Rock River Bay							
8-29	10.0	10.0	10.0	10.0	10.0	10.0	---
9-7	8.0	8.0	8.0	7.0	6.5	6.0	---
Beaver Bay							
8-29	8.0	8.0	7.5	7.0	6.5	5.5	5.5
9-14	12.5	12.5	12.5	12.5	12.5	12.5	8.5
No-Name Bay							
9-1	11.0	11.0	11.0	10.5	9.5	9.5	---
9-14	13.0	13.0	13.0	13.0	13.0	13.0	---
Sugar Loaf Cove							
8-31	7.0	7.0	6.5	6.0	6.0	5.5	---
9-7	7.5	7.5	7.5	6.5	6.5	6.1	---
Tofte							
8-31	11.0	11.0	11.0	9.5	9.5	9.0	8.5
9-7	10.8	10.8	10.5	10.5	9.5	8.6	8.0
Lutsen							
8-31	12.5	12.5	12.5	12.0	11.5	11.5	10.0
9-7	13.0	13.0	12.5	12.5	10.0	10.0	9.0
Good Harbor Bay							
8-31	11.5	11.5	11.0	9.0	8.5	8.5	7.8
9-7	11.5	11.5	11.0	10.0	10.0	9.5	9.5
Grand Marais							
8-31	9.5	9.5	9.5	9.0	9.0	8.5	8.5
9-7	10.5	10.5	10.0	10.0	10.0	9.2	9.0

tion center. It is possible that sewage effluent found its way into Grand Marais Bay. Rather extensive growths of Ulothrix sp. were noted in very shallow water. This green alga also appeared in the counts. Split Rock River Bay and Good Harbor Bay, on the other hand, were quite isolated and their high counts cannot be explained on the same basis as those of Grand Marais.

Neil and Owen (1964), in their paper on Cladophora in the Great Lakes, state that this green alga causes nuisance problems in Lake Erie and Lake Ontario. In this study, Cladophora was observed only at the Lester River. This growth may have been stimulated by the intermittent discharges of raw sewage directly into the lake near the sampling area. Such discharges have been observed following storms. Neil and Owen feel that increased nutrient levels, often as a result of added sewage, cause excessive growths of Cladophora. At Lester River, however, the growth could not be considered to be of nuisance proportions.

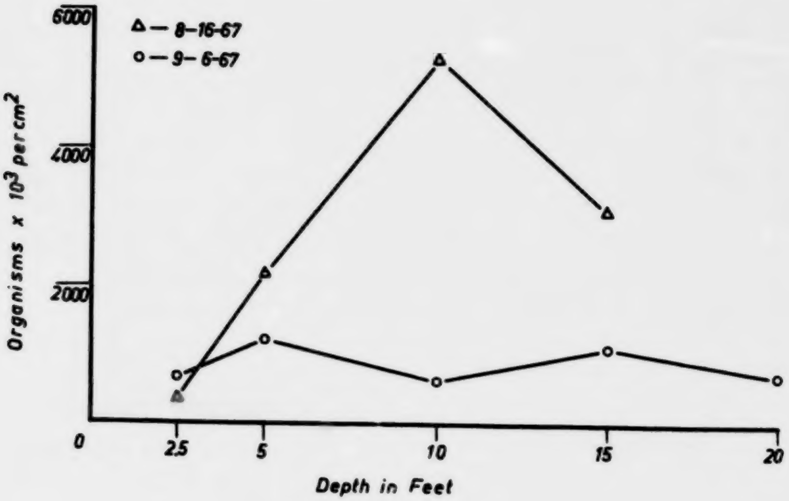

Figure 65. Naturally occurring periphyton, total counts, Lester River area, north shore, Lake Superior, 1967.

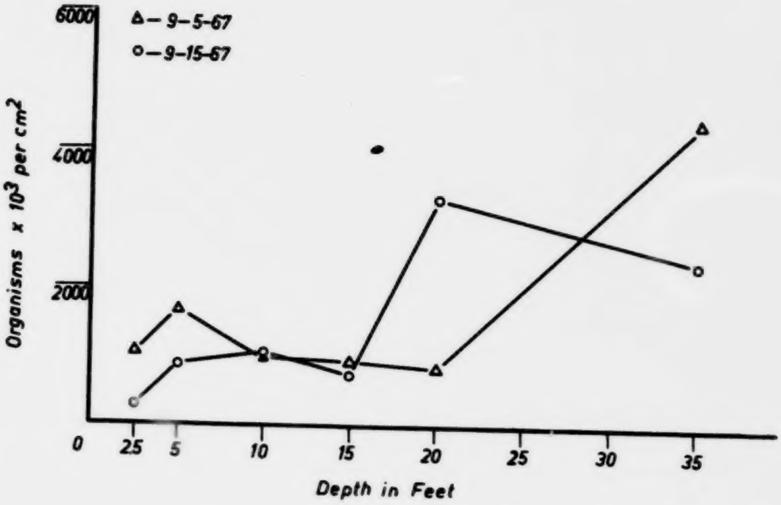

Figure 66. Naturally occurring periphyton, total counts, Knife River area, north shore, Lake Superior, 1967.

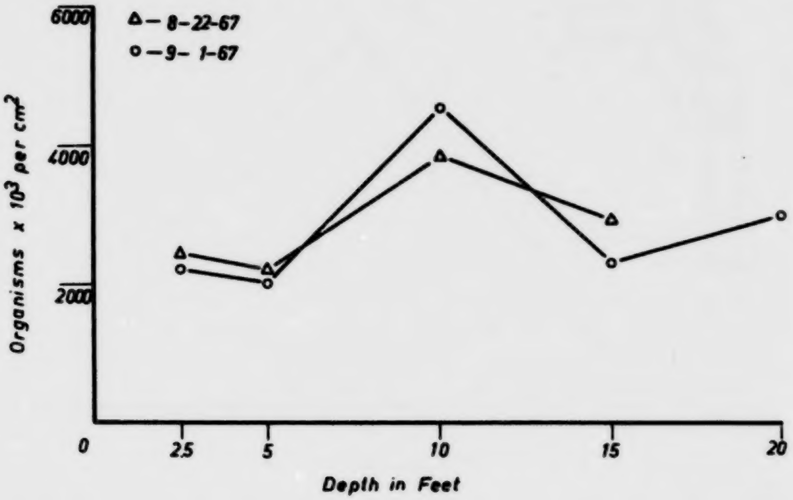

Figure 67. Naturally occurring periphyton, total counts, Burlington Bay, north shore, Lake Superior, 1967.

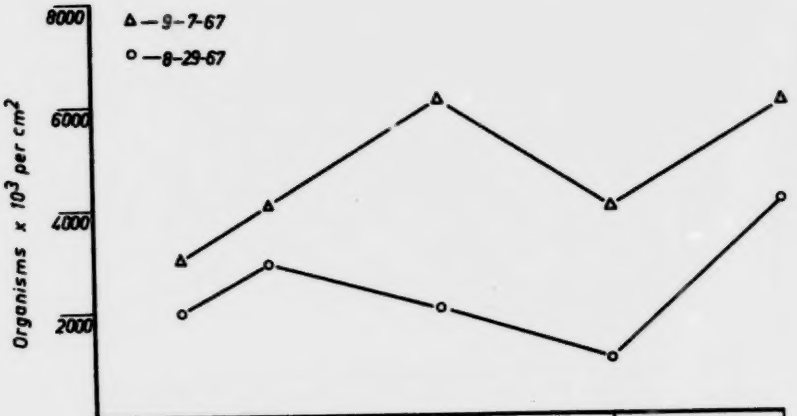

Figure 68. Naturally occurring periphyton, total counts, Split Rock River Bay, north shore, Lake Superior, 1967.

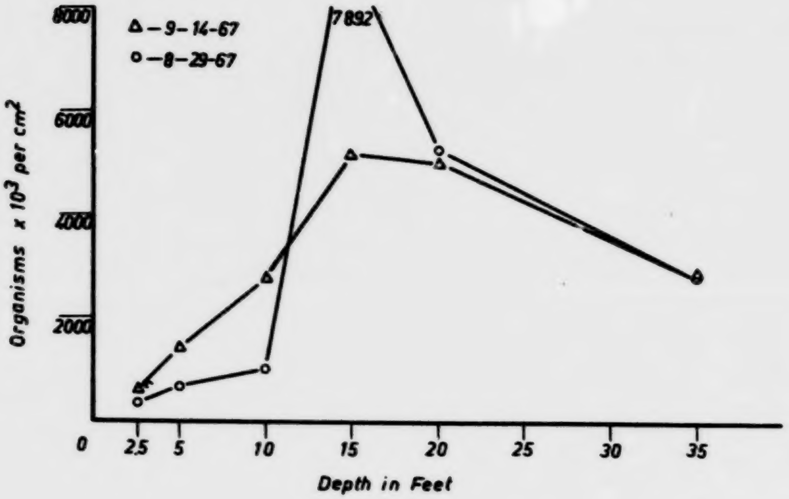

Figure 69. Naturally occurring periphyton, total counts, Beaver Bay, north shore, Lake Superior, 1967.

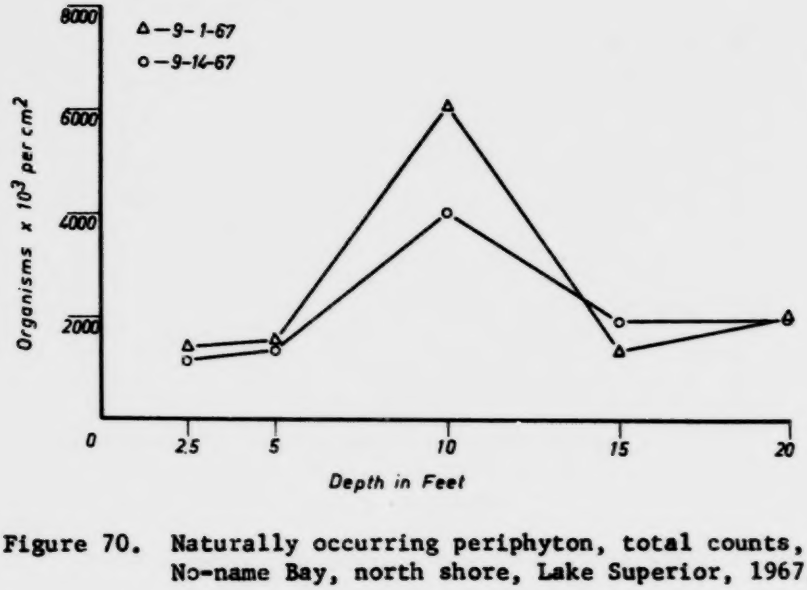

Figure 70. Naturally occurring periphyton, total counts, No-name Bay, north shore, Lake Superior, 1967.

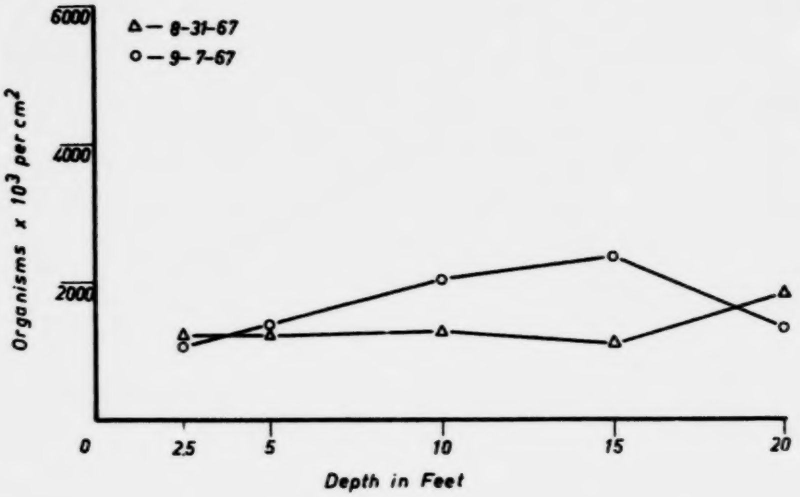

Figure 71. Naturally occurring periphyton, total counts, Sugar Loaf Cove, north shore, Lake Superior, 1967.

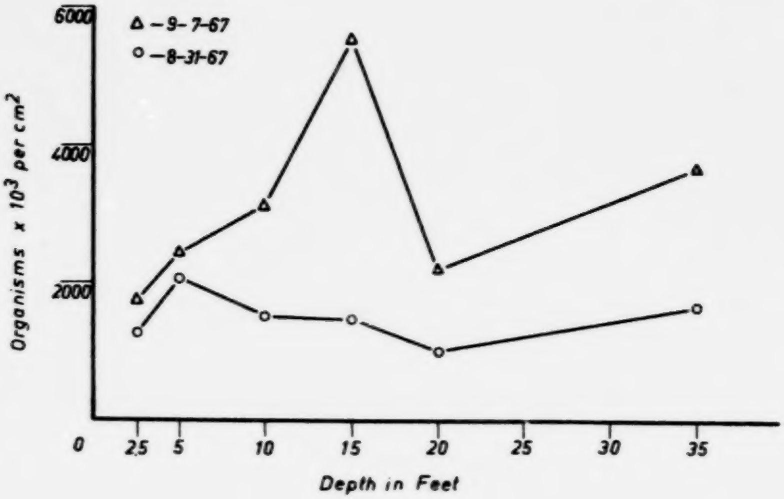

Figure 72. Naturally occurring periphyton, total counts, Tofte area, north shore, Lake Superior, 1967.

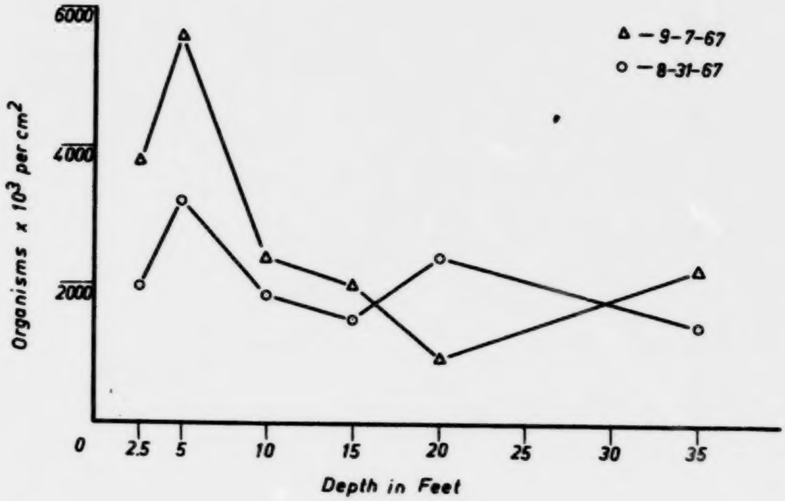

Figure 73. Naturally occurring periphyton, total counts, Lutsen area, north shore, Lake Superior, 1967.

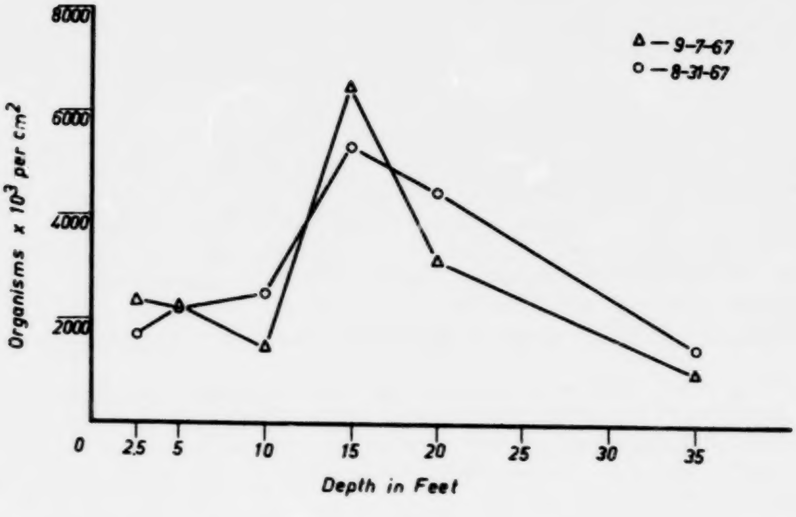

Figure 74. Naturally occurring periphyton, total counts, Good Harbor Bay, north shore, Lake Superior, 1967.

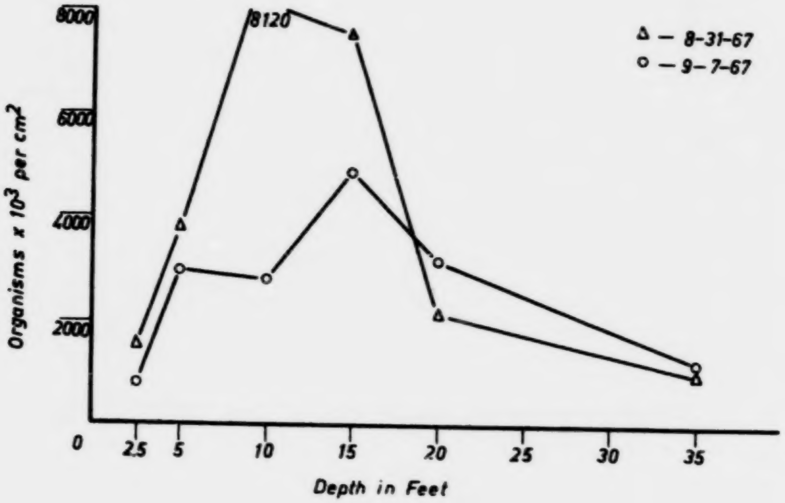

Figure 75. Naturally occurring periphyton, total counts, Grand Marais area, north shore, Lake Superior, 1967.

At Beaver Bay, which is close to the taconite operation at Silver Bay, black magnetic particles (ten to twenty microns in diameter) were observed. These did not seem to interfere with periphyton growth, for the counts were quite high (2,964,000/cm.^{2}). Interestingly enough, the highest periphyton productivity, in terms of weight, occurred at Beaver Bay.

At all eleven stations, four of the five most common organisms were *Synedra acus*, *Achnanthes microcephala*, *Cymbella* spp., and *Navicula* spp. The predominant organisms were always *Synedra acus* and *Achnanthes microcephala*. At the Lester River and at Sugar Loaf Cove, *Achnanthes microcephala* was the most common. At all other points, *Synedra acus* precominated. Occasionally appearing among the five most common organisms were *Nitzschia* spp., an unidentified blue-green (probably a small species of *Oscillatoria*), *Synedra ulna*, *Gomphonema* spp., and *Ceratoneis arcus*.

The five most common organisms in 1967 samples from Stony Point Bay were, in order, *Synedra acus*, *Achnanthes microcephala*, *Navicula* spp., *Cymbella* spp., and *Gomphonema* spp. Thus it can be seen that the organisms comprising the periphyton remain practically the same for a 107 mile segment of the north shore.

It is felt that the same factors which affect periphyton growth in Stony Point Bay influence growth at any other point in the lake. These are primarily water movement (regardless of cause), light intensity, temperature, available nutrients, and the type of substratum. While it is true that all of these factors are variable, the similarity found between the periphyton at Stony Point Bay and the eleven north shore stations indicate that these factors did not, at the time of this survey, differ drastically from point to point in the stretches of Lake Superior shoreline studied.

Summary and Conclusions
Taxonomy and Distribution of Periphyton

On the basis of the results obtained in this, the first portion of our Periphyton Study in the western arm of Lake Superior, it is concluded that the organisms found in the periphyton of the western arm of Lake Superior are indicative of clean water. The extensive shallow water area of Lake Superior supports large quantities of attached algae, which, as primary producers, form the first link in the food chain. It is felt that the results of this study will be of practical value in the future. Since the periphyton is fixed in one place, it reflects the quality of water masses with which it comes into contact. By using the results of this study as baseline data, it will be possible in the future to determine the qualitative and quantitative changes that occur in the periphyton as a result of eutrophication. It is hoped that, in this way, subtle changes in water quality brought about by chemical or thermal pollution can be detected.

Some of the specific observations which can be reported here in the nature of a summary are:

(1) The plant portion of the periphyton found attached to rocks consists almost solely or representatives from three phyla of algae namely the Chrysophyta, the Chlorophyta and the Cyanophyta.

(2) Most abundant in terms of numbers of organisms is the phylum Chrysophyta, and diatoms make up over ninety per cent of this group.

(3) The genera of diatoms which were predominant in the periphyton growth were Synedra, Achnanthes, Navicula, Cymbella and Gomphonema.

(4) Mean total counts of organisms in the naturally occurring periphyton of Stony Point Bay, the primary sampling area, ranged from 497,000 per square centimeter of rock surface in 1966 to 1,470,000 per square centimeter in 1967.

(5) The biomass of the naturally occurring Stony Point Bay periphyton, in terms of dry weight, was 153 grams per square meter in 1965, 104 g./m.^{2} in 1966, and 156 g./m.^{2} in 1967.

(6) After forty-six days of regrowth on artificially denuded rocks in Stony Point Bay, the growth level reached finally was approximately eighteen per cent of that occurring naturally.

(7) The daily regrowth production rate in Stony Point Bay averaged 3.6 grams of dry weight per square meter and 0.067 grams of organic weight (ash-free dry) per square meter.

(8) Mean total counts of organisms from eleven north shore stations ranged from 1,466,000 organisms per square centimeter at Sugar Loaf Cove to 3,798,000 per square centimeter at Split Rock River Bay.

(9) The interrelated factors which affect periphyton growth are light intensity, water movement, depth, temperature, nutrient levels, and type of substratum.

(10) The periphyton of Lake Superior was found to be similar, in many respects, to attached growths found in streams.

Section VI

The Photosynthetic Pigments of Periphyton and Periphyton Productivity

Results and Discussion

Since this portion of the study was carried out over a period of three consecutive summers, we have, in the interest of simplicity and clarity chosen to present the results of the investigation in a chronological order. In 1966 for example, while some quantitative data were accumulated, time was spent largely in the development of methods. The 1967 season, on the other hand, represents the period devoted primarily to a sampling program, and 1968 was the year for special studies intended to provide answers for special problems which had become apparent in the course of our 1966 and 1967 studies. The results of the 1968 laboratory experiments were needed to convert the data collected earlier under standard conditions to a form more nearly approximating the actual situation in the lake.

In the interest of brevity and clarity, this chapter includes discussion of results along with the presentation of data. The data have been combined and summarized in various ways and are presented in the form of figures and tables. The discussion involves general interpretation of the data, comparisons between results of the three summers and between various sampling areas, and correlations between the several parameters employed in the study of periphyton. When possible, results will be compared with data reported from other studies of periphyton communities. An attempt also will be made to establish the relative importance of the periphyton community as a primary producer in Lake Superior when a comparison is made with the productivity of the phytoplankton.

The area in which the major part of the study was concentrated was Stony Point Bay which has been described in detail in an earlier section of this report. As will be remembered most of the bottom in this bay was covered by rocks, with very small and scattered sand patches breaking up the rocky areas. Portions of the bay floor are, to be sure, designated on maps by the word "sand" but even here patches of rocks were encountered. In general the rocks ranged in size from one inch to five or six feet in diameter, but most of the bottom was covered by rocks ranging from four to twelve inches in diameter. The triangular sampling area, bounded by a reference buoy 2336 feet from shore, the Little Sucker River on the southwest, and Stony Point on the northeast, was found to encompass 321,000 square meters.

Stony Point Bay is located in a sparsely populated area and is not easily accessible from the adjacent land because the banks leading to the water's edge are very steep. The only persons encountered in the bay area were commercial fishermen who came by boat to tend small fishnet cribs which were permanently located in the bay. Because of past experiences with net fouling these fishermen expressed considerable interest in the project and welcomed the technicians who carried out the field work.

Turbidity in the water of the bay was quite variable and was considerably affected by flow from the Little Sucker River. During and following stormy periods, heavy suspensions of silt were carried into the bay from the mouth of the river, whereupon the materialwas often carried across the bay in an easterly direction.

Ruschmeyer and Olson (1957) have shown the general circulation of water in the western arm of Lake Superior to be counterclockwise. However, winds and eddy effects can cause a reversal of flow near shore in certain areas.

Under more normal conditions periphyton organisms and silt from the shore area were also suspended in the bay by water agitation when wave action was severe. Secchi disc readings varied considerably, the maximum being approximately eight meters. Occasionally, the water was clear enough that the bottom could be viewed from the surface in depths up to twenty feet. Water color as viewed from shore was usually greenish, but atmospheric conditions and turbidity sometimes accounted for a tan or grey appearance.

A heavy, brown layer of periphyton was usually apparent on the rocks and sand in the bay. Where the periphyton was not disturbed by wave action, small gas bubbles could be seen entrapped in the wooly growth. Occasionally, divers reported viewing small fish near the bottom of the bay; these fish were found to be sculpins. Small groups of crustaceans, identified as Mysis relicta, were sometimes present. Mayfly nymphs, midge larvae, caddisfly larvae, nematodes, snails and leeches also were found in association with the periphyton on the rocks. A few clumps of the macroscopic, filamentous green alga, Nitella, were encountered on rare occasions.

The rocks taken from Stony Point Bay differed somewhat from one another in appearance when the periphyton was removed. An analysis of one hundred of these rocks revealed that twenty-two lithic types were represented in the bay. The predominant type was found to be basalt, of which twenty-four per cent were andesite and diabase. Fourteen of the one hundred were diabase, while seven were porphyritic trachyandesite to mafic quaryz latite.

Findings in 1966

Data presented represent that portion of the study which was carried out between August 9 and September 6. During this twenty-nine day sampling period, east or northeast winds occurred on eleven days, or thirty-eight per cent of the time. The average velocity was fifteen miles per hour. These winds caused very rough water, making it impossible to safely navigate the two miles from Knife River Harbor to Stony Point Bay. For this reason, only five sampling trips were completed.

However, in the course of these five trips, a total of eighty-one rocks were obtained from depths of 2.5, 5, 10, 15, 20, and 35 feet.

The average periphyton pigment concentrations per unit area of rock surface are plotted against sampling depth in Figure 76. Maximum, minimum, and mean concentrations are presented in Table XIX. Since the quantity of phytoplankton pigments, in the small amounts of water collected along with the rocks in the plastic bags, proved to be negligible when compared with that of the periphyton, no correction for this factor was necessary. All pigments of the periphyton collected from depths of ten through thirty-five feet decreased considerably during the sampling period; this trend was not shown by samples taken at depths of 2.5 and five feet. From Table XIX and Figure 76, it can be seen that chlorophyll a was the predominant pigment in nearly all samples. The minimum mean concentration was 0.190 milligrams per 100 square centimeters of rock surface at a depth of 2.5 feet, while the maximum mean concentration reached 0.510 milligrams per 100 square centimeters at a depth of thirty-five feet. Chlorophyll c and non-astacin carotenoids were present in somewhat lower concentrations, attaining minima at the same depth and maxima at different depths (see Figure 76). The minimum mean chlorophyll c concentration, 0.068 MSPU per 100 square centimeters, appeared at a depth of 2.5 feet and the maximum, 0.340 MSPU per 100 square centimeters, at a depth of thirty-five feet. The lowest mean concentration of non-astacin carotenoids was encountered at 2.5 feet (0.132 MSPU/100 cm^2) and the highest at twenty feet (0.311 MSPU/100 cm^2).

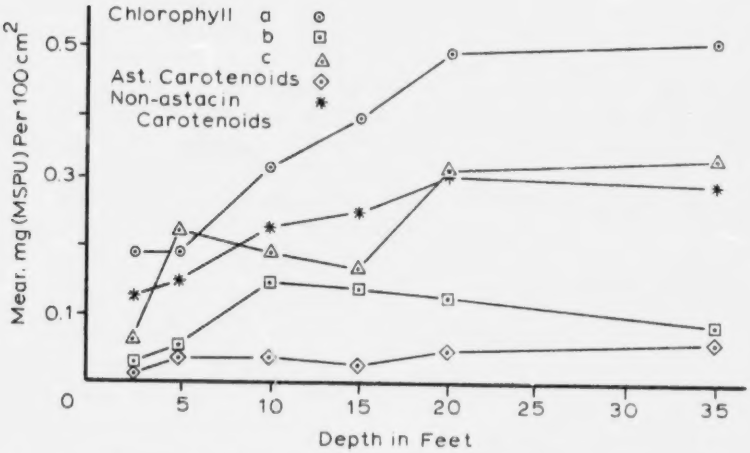

Figure 76. Average Periphyton Pigment Concentrations (per unit area of rock surface) at Standard Sampling Depths, Stony Point Bay, Lake Superior, 1966.

The observed ratio of chlorophyll a : chlorophyll c : non-astacin carotenoids, approximately 5:3:3, is to be expected because of the overwhelming preponderance of diatoms in the samples. In Section V reference was made to the fact that six genera, Achnanthes, Synedra, Cymbella, Navicula, Cocconeis, and Gomphonema, accounted for over ninety per cent of the organisms in samples from all depths. The ratio of chlorophyll c/chlorophyll a at the 2.5-foot depth was 0.35; at five feet, 1.10; at ten feet, 0.61; at fifteen feet, 0.51; at twenty feet, 0.64; and at thirty-five feet, 0.67. No trend is apparent. The ratio of non-astacin carotenoids/chlorophyll a was more constant with depth. At a depth of 2.5 feet, the ratio was 0.67; at five feet, 0.76; at ten feet, 0.73; at fifteen feet, 0.74; at twenty feet, 0.63; and at thirty-five feet, 0.58. The ratio seems to decrease slightly as depth increases. The sampling period was not long enough to indicate any seasonal trends as far as the pigment ratios are concerned.

Chlorophyll b and astacin carotenoids were present in smaller amounts. Chlorophyll b reached a minimum of 0.036 milligrams per 100 square centimeters at a depth of 2.5 feet and a maximum of 0.158 milligrams per 100 square centimeters at a depth of ten feet; the minimum astacin carotenoid value, 0.015 MSPU per 100 square centimeters, appeared at 2.5 feet and the maximum, 0.061 MSPU per 100 square centimeters, at thirty-five feet. The chlorophyll b peak corresponds to a drop in chlorophyll c concentration (Figure 76), possibly indicating the presence of a relatively higher number of periphytic green algae at depths of ten and fifteen feet than at other depths. This hypothesis was not borne out by the routine microscopic examination, as little difference was seen in the numbers of green algae at the various depths; however, it is possible that with the use of a random field counting method and a 200X magnification, some small green algae might be missed in a heavy sample. After careful re-examination of several samples, it was concluded that the reported percentage of green algae was, in fact, low.

The minute but persistent astacin carotenoid values observed may be attributable to the presence of animal grazers in the samples. Little difference can be seen in the concentrations at various depths; the minimum and maximum concentrations during the sampling period correspond in general with those of the other pigment groups. Part of the apparent astacin carotenoid value may be the result of an error in the formulas of Richards and Thompson (1952). This possible error (suggested by Parsons and Strickland, 1963) is due to the production of a positive animal carotenoid value by the plant xanthophyll, fucoxanthin.

Further inspection of Figure 76 reveals that all of the periphyton pigments tend to increase on a unit area basis from the shallow to the deeper parts of the bay. However, this increase is not due to a proportional rise in numbers of organisms with depth (see Figure 77). Although peaks occur at fifteen or twenty feet, it will be seen that when the amount of each pigment per 100,000 organisms is plotted against depth, the same general increase in concentration occurs with

TABLE XIX

PIGMENT CONCENTRATIONS OF NATURALLY OCCURRING PERIPHYTON FROM STANDARD DEPTHS, STONY POINT BAY, LAKE SUPERIOR, 1966. MILLIGRAMS OR MSPU PER 100 CM^2 ROCK SURFACE

	Depth in feet					
	2.5	5	10	15	20	35
Chlorophyll *a*						
Max.	0.232	0.275	0.729	0.803	1.399	0.969
Min.	0.125	0.120	0.136	0.096	0.139	0.277
Mean	0.191	0.198	0.328	0.338	0.491	0.510
Chlorophyll *b*						
Max.	0.054	0.094	0.430	0.421	0.450	0.304
Min.	0.012	0.001	0.010	0.015	0.017	0.001
Mean	0.040	0.058	0.158	0.149	0.134	0.090
Chlorophyll *c*						
Max.	0.091	0.517	0.733	0.404	0.778	1.060
Min.	0.027	0.010	0.010	0.011	0.091	0.103
Mean	0.066	0.197	0.199	0.171	0.316	0.340
Non-astacin carotenoids						
Max.	0.152	0.211	0.530	0.520	0.860	0.595
Min.	0.110	0.089	0.091	0.090	0.088	0.152
Mean	0.130	0.153	0.237	0.255	0.312	0.297
Astacin carotenoids						
Max.	0.027	0.096	0.143	0.076	0.130	0.183
Min.	0.001	0.001	0.010	0.008	0.017	0.020
Mean	0.015	0.044	0.046	0.032	0.053	0.061

depth. Therefore, higher pigment concentrations in the individual organisms were found to correspond directly to decreasing light intensity. The peaks observed at fifteen or twenty feet could be explained on the basis that larger aliquots were used to compensate for a relative scarcity of organisms present on the rocks from these depths. Such aliquots, when fine colloidal clay is present, may lead to slightly increased absorption readings, as centrifugation of the colloidal clay is difficult. If an adjustment is made for this factor, the amount of pigment per organism when plotted against increasing depth will approximate a sigmoid curve which reaches an asymptote at fifteen or twenty feet. It was assumed that the higher pigment concentrations in deeper water were a result of conditioning to a lower light intensity. This "sun and shade" reaction has been reported on several occasions as a phenomenon occurring in phytoplankton populations (Kozminski, 1938; Burkholder and Sieburth, 1961); however, the conditioning is much more apprent in the Stony Point Bay periphyton, because organisms attached at one depth must remain at that depth unless broken loose by violent currents, and are not continually mixed as phytoplankton organisms are. Thus the periphyton growing at a certain depth has a greater opportunity to adjust to light intensity than does the phytoplankton.

In order to compare the results of chlorophyll analyses performed with a broad spectrum instrument with those based on readings from a narrow-band spectrophotometer, the observed chlorophyll a, b and c concentrations (DK-2A) were added together and plotted against depth along with the Klett-Summerson total chlorophyll concentration values (Figure 78). The chlorophyll results based on readings with the Klett-Summerson colorimeter were considerably lower than the corresponding total chlorophyll concentrations obtained with the DK-2A method. This discrepancy may be due to the fact that the Klett #66 filter allows the passage of light only in the 640 to 700 millimicron range, thus effecting no measurement of chlorophyll c, which does not absorb visible light of wavelength greater than 635 millimicrons. Therefore, these observations do not lend support to the contention by Parsons and Strickland (1963) that Richards' formulas yield chlorophyll values which are too high. The data from the six standard sampling depths show that the narrow-band instrument produced total chlorophyll figures which averaged 1.7 times as high as those from the broad spectrum instrument. This factor, when calculated on the basis of data from each depth, varied from 1.49 to 1.90. It is interesting to note that the two methods agreed best on samples from 2.5 and fifteen feet, where the amounts of chlorophyll c were lowest in relation to the other pigments.

Many investigators have reported chlorophyll concentrations on a unit area basis as a reflection of the general magnitude of biomass. In order to compare the data from Stony Point Bay with those reported for certain other ecosystems, the total chlorophyll values obtained by the DK-2A method were converted to grams per square meter (see Table XX). These values ranged from 0.0297 at the 2.5-foot depth to 0.0941 at the twenty-foot depth. The average from the entire bay was 0.0660. Table XX includes values calculated for some ecosystems studied by other

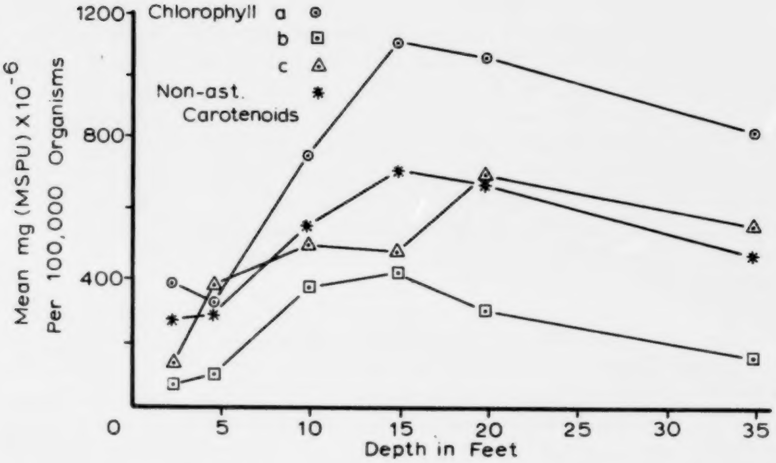

Figure 77. Average Periphyton Pigment Concentrations (per 100,000 Organisms) at Standard Sampling Depths, Stony Point Bay, Lake Superior, 1966.

workers. Those figures range from 0.006 grams of chlorophyll per square meter in a Japanese lake (Ichimura, 1954) to 0.6 grams per square meter, the upper limit reported for the phytoplankton of Long Island Sound by Riley (1956). The mean concentration for Stony Point Bay (0.0660) fits nicely within the range calculated for a rocky stream in Utah (McConnell and Sigler, 1959). It should be noted that since the reported concentrations for Stony Point Bay are based on surface area of rocks which protrude above the bay floor, these figures cannot be compared directly with concentrations based on a unit area of water surface. The total surface area of the rocks in Stony Point Bay is greater than the area of the water surface above. Therefore, in directly comparing chlorophyll concentrations of phytoplankton with those of the periphyton within a given region, an allowance must be made for this factor.

Photosynthetic rate as measured by the Gilson respirometer was shown to be lowest for samples taken from a depth of 2.5 feet (39 microliters of oxygen evolved per square centimeter of rock surface per hour) and highest for samples from five feet (85 micro-liters of oxygen evolved per square centimeter per hour). Values obtained from samples taken from ten, fifteen, twenty, and thirty-five foot depths fell consistently between fifty and sixty microliters of oxygen evolved per square centimeter per hour (see Figure 79). These values represent gross photosynthetic rate at 20° centigrade and a light intensity of 1500 foot-candles, and do not account for losses due to respiration. The mean value for the five-foot depth was influenced greatly by a single very high reading on one sampling day and is probably higher than the true average for the

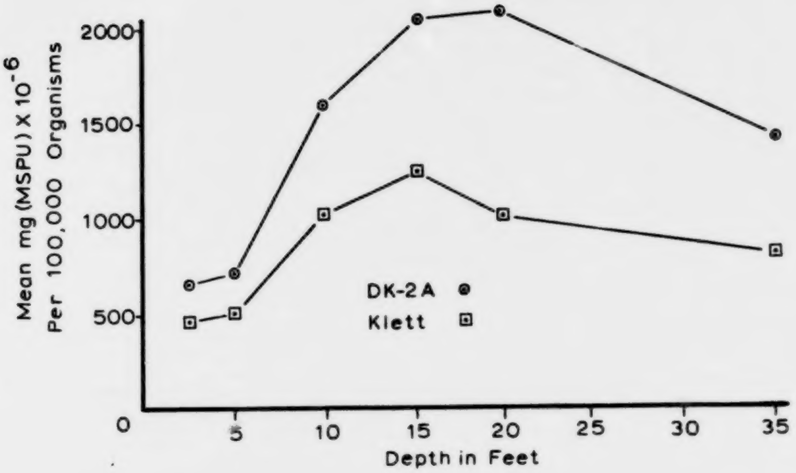

Figure 78. Periphyton Total Chlorophyll Concentrations as Measured by a Broad-Spectrum Colorimetric Method, and by a Narrow-Band Spectrophotometric Method.

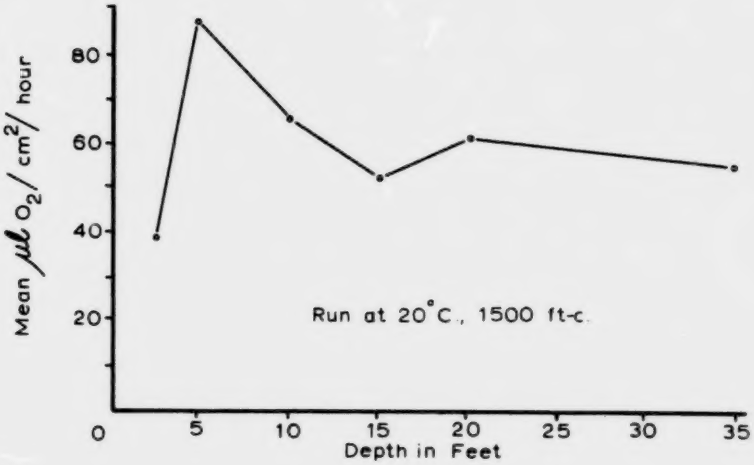

Figure 79. Average Gross Photosynthetic Rates (per unit area) for Samples from Standard Depths, Stony Point Bay, Lake Superior, 1966; Run at 20° C., 1500 Foot-Candles.

TABLE XX

CHLOROPHYLL CONTENT OF STONY POINT BAY PERIPHYTON (1966) AND OTHER COMMUNITIES ON A UNIT AREA BASIS

Investigator	Ecosystem	Chlorophyll (G/M^2)
	Stony Point Bay Periphyton	
	2.5'	.0297
	5'	.0453
	10'	.0685
	15'	.0658
	20'	.0941
	35'	.0940
	Average	.0660
Riley (1956)	Long Island Sound phytoplankton	0.1 - 0.6
Odum and Odum (1955)	Coral reef	0.5
Ichimura (1954)	Japanese lake	0.006
McConnell and Sigler (1959)	Rocky stream	0.05 - 1.0

sampling period. This probable error is borne out by the photosynthesis/respiration ratios (Table XXI). The ratio for the five-foot sample (4.40) is inconsistent with the values calculated for samples from the other depths (3.03 to 3.43) and the 1967 data subsequently showed that no significant peak occurs at five feet. The P/R ratio for the five foot samples during that year was 3.46, while the ratio for the other depths ranged from 2.96 to 3.36.

The overall mean P/R ratio for Stony Point Bay periphyton under the test conditions was found to be 3.39. Published data relating the photosynthetic and respiration rates of periphyton are rare. However, a striking comparison may be made between the average P/R ratio for Stony Point Bay periphyton (3.39) and that calculated from the data of Jackson (1966) for Cladophora fracta in Lake Ontario (3.42). Riley's (1957) data for the algae of the Sargasso Sea yield a P/R value of 3.06. A value of 2.91 has been calculated for the photosynthetic organisms of Silver Springs, Florida (Odum, 1957).

Since the P/R ratios for samples from all depths in Stony Point Bay are similar except for the five-foot samples, the net photosynthetic rates follow nearly the same pattern as the gross rates (Table XXI). The net rates ranged from 27.5 microliters of oxygen evolved per square centimeter of rock surface per hour for the samples from 2.5 feet to 67.9 microliters of oxygen per square centimeter per hour for the five-foot samples. Values for the remaining depths varied between 35.9 and 45.3. The overall mean rate for net photosynthesis in samples from all depths was 43.3 microliters of oxygen evolved per square centimeter per hour.

Assuming fifteen hours of daylight per day, the photosynthetic rates were converted to production rates in terms of carbon fixed (Table XXI). Net production varied between 1.62 grams of carbon fixed per square meter per day at a depth of 2.5 feet and 4.49 grams of carbon fixed per square meter of rock surface per day at five feet; the average value for all sampling stations was 2.63 grams of carbon fixed per square meter per day. These values take into account losses due to daytime and nighttime respiration, and represent true net production figures under the test conditions. The figures were again converted to reflect net production in terms of organic matter. For purposes of calculation, it was assumed that all carbon was fixed in the form of glucose (see Table XXI). Thus the production rates ranged from 4.05 grams production (as glucose) per square meter per day to 11.22 grams per square meter per day; the average rate for samples from all depths was 6.58 grams (as glucose) per square meter per day. Again, these values are corrected for respiration losses and are net production rates for the test conditions (20° C., 1500 foot-candles)

TABLE XXI

PHOTOSYNTHESIS DATA FOR PERIPHYTON SAMPLED AT DIFFERENT DEPTHS, STONY POINT BAY, 1966; RUN AT 20° C., 1500 FOOT-CANDLES

	Sampling depth in feet						
	2.5	5	10	15	20	35	Mean
Gross Photosynthesis							
ul $O_2/cm^2/hr$	+39.7	+87.9	+66.3	+53.6	+61.5	+55.6	+60.7
Respiration							
ul $O_2/cm^2/hr$	-12.2	-20.0	-21.0	-17.7	-17.9	-16.0	-17.3
Net Photosynthesis							
ul $O_2/cm^2/hr$	+27.5	+67.9	+45.3	+35.9	+43.6	+39.6	+43.4
P/R	3.26	4.40	3.14	3.03	3.43	3.10	3.39
Net production							
Grams carbon fixed per M^2 per day	1.62	4.49	2.63	2.03	2.64	2.41	2.63
Grams (as glucose) per M^2 per day	4.05	11.22	6.57	5.07	6.60	6.02	6.58

TABLE XXII

PERIPHYTON VOLUMES AND DRY WEIGHTS AT THE STANDARD DEPTHS, STONY POINT BAY, LAKE SUPERIOR, 1966

		Depth in feet					
		2.5	5	10	15	20	35
Dry Weight (Mg. per cm^2 rock surface)	Max.	10.0	15.1	19.7	30.0	32.0	24.3
	Min.	2.5	3.1	5.1	6.0	2.1	5.3
	Mean	6.5	7.1	10.7	14.0	13.4	11.6

(continued next page)

TABLE XXII (continued)

	Depth in feet					
	2.5	5	10	15	20	35
Volume (Ml. per 100 cm^2)	3.35	2.98	9.27	8.55	4.89	6.74
	2.62	2.20	2.29	1.72	2.80	1.85
	3.00	2.56	4.05	3.71	3.36	3.98

An interesting relationship between oxygen yield, chlorophyll concentration and sampling depth is suggested by Figure 80. The volume of oxygen evolved per milligram of total chlorophyll begins at 13.5 x 10^3 microliters per hour at 2.5 feet, rises to 22.3 x 10^3 microliters per hour at five feet, and then falls off asymptotically through the remaining depths. If the five-foot value is ignored (this figure is probably too high), a smooth, slowly descending curve is produced. If photosynthetic rate increases proportionately with increased pigment concentration, then the oxygen:pigment ratio should approximate a constant value in all samples, regardless of their source, when the samples are exposed to excess light. However, recalling that pigment concentrations were shown to increase with depth, and noting from Figure 80 that the oxygen: pigment ratio is not constant for organisms taken from different depths, one may assume that once a certain low light level is reached, the further addition of pigments by an algal cell in decreased light will not necessarily maintain the expected photosynthetic rate. Apparently, conditioning to a certain light intensity affects the photosynthetic capacity of a pigment unit as well as influencing pigment concentrations. This factor is important in the consideration of the effects of short-term and long-term increases in turbidity on periphyton productivity, whether such turbidity is caused by natural runoff from the land or by advancing water pollution.

The photosynthesis and chlorophyll data from Figure 80 were also calculated as grams of carbon fixed per gram of chlorophyll so that comparisons of these "assimilation numbers" could be made with those reported elsewhere for other communities. The assimilation value determined for Stony Point Bay at a depth of 2.5 feet was 7.2 grams of carbon fixed per hour per gram of chlorophyll; at five feet, 11.9; at ten feet, 4.8; at fifteen feet, 3.7; at twenty feet and thirty-five feet, 3.2. The average of these figures is 5.7 grams of carbon fixed per hour per gram of chlorophyll. Discarding the five-foot value, which is probably in error as previously explained, the average becomes 4.4. This figure compares quite well with the 3.7 reported by Ryther and Yentsch (1957) for marine phytoplankton. It is, however, considerably higher than assimilation numbers calculated for various ecosystems by certain other workers. For example, Ichimura (1954) reported 2.36 grams of carbon fixed per hour per gram of chlorophyll in Lake Suwa, Japan. Odum and Odum (1955) found the value for a coral reef to be 1.5, while the data of McConnell and Sigler (1959) show 0.75 grams of carbon fixed per hour per gram of chlorophyll in a rocky stream in Utah.

The dry weights of the 1966 periphyton samples are presented in Table XXII. The average weights correlate rather well with the pigment concentrations, but this relationship may be purely coincidental. Since the relationship between pigment concentrations and numbers of organisms has been shown to depend on the depth from which the sample was taken, there is reason to believe that the amount of pigment per unit of dry weight would also vary from one depth to another. The mean dry weight was lowest at the 2.5-foot depth (6.5 milligrams per square centimeter of rock surface) and highest at the fifteen-foot depth (14.0 milligrams per square centimeter). The total number of organisms was lowest at fifteen feet (Fox et al., 1967). The weight of the periphyton was less at thirty-five feet than at the intermediate depths. This pattern can be explained on the basis that the organisms near shore are sometimes removed from the rocks by wave action while the organisms in the deeper areas are not affected. The lower biomass at thirty-five feet is probably due to relatively low light intensity and temperature. Varying amounts of sand and silt accompanied the organisms in the samples; apparently, a larger proportion of sand and silt was present in the samples from the fifteen-foot depth than those from other depths. This point was borne out by visual examination of the samples. On the basis of the 1966 mean dry weights for all depths, the standing crop of periphyton in Stony Point Bay was calculated to be 104 grams per square meter or 37.1 tons for the entire bay.

The volumes of the settled periphyton samples are also shown in Table XXII. The mean values range from 3.00 milliliters of periphyton per 100 square centimeters of rock surface at the five-foot depth to 4.05 milliliters per 100 sqaure centimeters at the ten-foot depth. These results compare reasonably well with the dry weights, inasmuch as the volume determinations were also subject to the influence of sand and silt in the samples. Dry weight and volume determinations would appear to be useful in the estimation of the general magnitude of biomass in the periphyton community.

Enough quantitative data were gathered during the summer of 1966 to allow the formulation of certain tentative conclusions regarding the biomass of Stony Point Bay periphyton and the relationships between the various parameters which were observed. The periphyton pigments were dominated by chlorophyll a, with chlorophyll c and non-astacin carotenoids approximately equal as secondary pigments. Low chlorophyll b concentrations indicate the presence of a relatively low proportion of green algae to diatoms. It is apparent that the organisms increased their pigment concentrations in deeper water, probably in response to lower light intensity. Chlorophyll per square meter and carbon fixed per square meter were shown to be of the same order of magnitude as

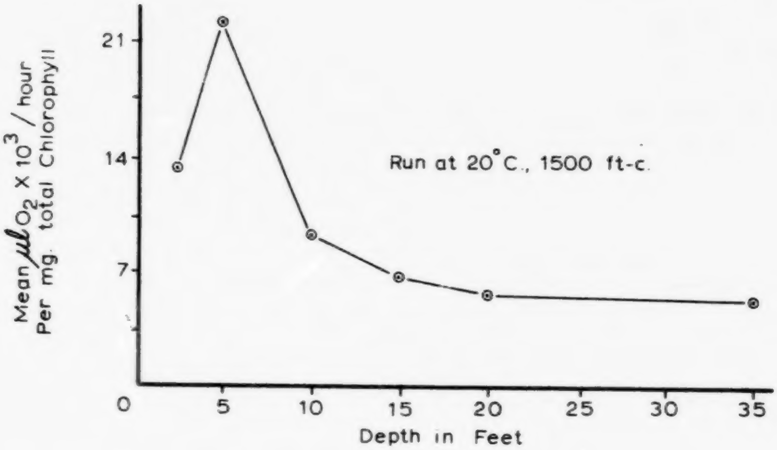

Figure 30. Average Periphyton Gross Photosynthetic Rates (per unit total chlorophyll) at Standard Sampling Depths, Stony Point Bay, Lake Superior, 1966.

for other ecosystems. Astacin carotenoid values, while quite low, probably reflect the association of certain animal forms with the periphytic algae. The data indicate that any single measurement, such as pigment analysis, enumeration of organisms, or the determination of weight, volume or photosynthetic rate, will probably now show the true productivity of the periphyton.

It was deemed necessary to confirm the 1966 results by obtaining more data on the same bay with similar techniques. In addition, the 1966 data raised a number of questions which could be answered only by a more extensive sampling program. Among these questions were the following: Are periphyton pigment concentrations actually so variable with depth as indicated by the 1966 data? Are there seasonal changes in concentration on an area basis, and do consistent differences in pigment ratios occur with depth? What is the relationship between organic weight, total dry weight and other parameters of biomass? Would further sampling confirm the apparent decrease in efficiency of the pigment unit as the pigments become more concentrated?

Findings 1967

The experience gained in sampling procedures and analysis during the 1966 season made a much more comprehensive program possible in 1967. Furthermore general observations in the field relative to conditions of growth and a multitude of other ecological factors provided a basis for better judgement relative to the interpretation of the findings made. The weather, too, during the summer of 1967, was more favorable and the sampling program was not seriously interrupted by storms. Greater emphasis should therefore be given to the data obtained during that year. For simplicity and hence for greater effectiveness, this chapter has been divided into three parts. The first section is concerned with the naturally occurring periphyton of Stony Point Bay, and the second with the regrowth study conducted in the same bay, while the third part deals with an investigation of the periphyton communities of north shore areas other than Stony Point Bay.

Naturally Occurring Periphyton, Stony Point Bay

Routine samples were collected in Stony Point Bay from July 11 to September 15, 1967. An additional sampling trip was made on November 10. The same procedures were used as in 1966 and during each sampling run three rocks were taken from each standard depth, namely 2.5, 5, 10, 15, 20 and 35 feet. Sampling was done twice a week and a total of 306 rocks were collected.

The pigment concentrations, on a unit area basis, for each depth are shown in Figure 81. Each point represents the average concentration of one pigment type at one depth during the entire sampling period. Chlorophyll a was the predominant pigment at all depths, ranging from a minimum mean concentration of 0.330 milligrams per 100 square centimeters of rock surface at a depth of fifteen feet to a maximum of 0.976 milligrams per 100 square centimeters at a depth of 2.5 feet. The mean concentration for samples from the thirty-five foot depth was 0.583 milligrams per 100 square centimeters. The same pattern was exhibited by the other plant pigment groups. The chlorophyll c concentration began at 0.386 MSPU per 100 square centimeters at a depth of 2.5 feet, fell to 0.163 MSPU per 100 square centimeters at fifteen feet, and then rose to 0.298 MSPU per 100 square centimeters at thirty-five feet. The non-astacin carotenoid values were similar in magnitude, varying from 0.475 MSPU per 100 square centimeters at the 2.5 foot depth to 0.132 MSPU per 100 square centimeters at fifteen feet. At the thirty-five foot depth, the mean concentration was 0.201 MSPU per 100 square centimeters. Chlorophyll b was present at all depths in considerably lower concentrations than the other plant pigments. The maximum chlorophyll b concentration appeared at a depth of 2.5 feet (0.146 milligrams per 100 square centimeters) while the minimum concentration occurred at fifteen feet (0.064 mg./100 cm.^{2}). The concentration at the thirty-five foot depth was intermediate in magnitude (0.096 mg./100 cm^2). Astacin carotenoids were present in small amounts, but did not follow the pattern of concentration exhibited by plant pigments in terms of sampling depth. The highest mean concentration of astacin carotenoids was found in samples from a depth of thirty-five feet (0.035 MSPU/100 cm^2) and the lowest in samples from 2.5 feet (0.015 MSPU/100 cm^2).

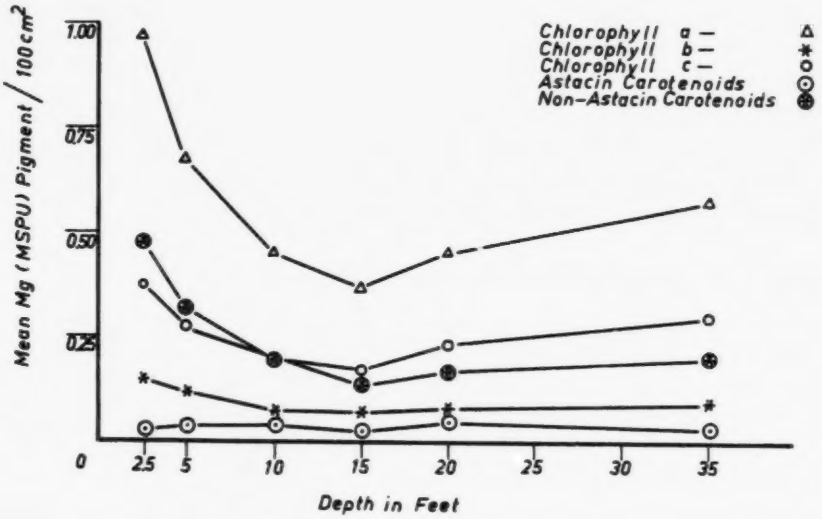

Figure 81. Average Periphyton Pigment Concentrations (per unit area of rock surface) at Standard Sampling Depths, Stony Point Bay, Lake Superior, 1967.

The curves representing the relationships between periphyton concentrations on an area basis and sampling depth in 1967 (Figure 81) bear little resemblance to those of 1966 (Figure 76). Differences in both shape and magnitude are obvious; however, it will be noted that the major differences occur only at depths from 2.5 feet to ten feet. The mean chlorophyll a concentration found at the 2.5 foot depth in 1967 (0.976 milligrams per 100 square centimeters) was more than five times as high as the corresponding figure for 1966 (0.191 mg./100 cm^2). The amounts of chlorophylls b and c and non-astacin carotenoids were four to five times higher at 2.5 feet in 1967 than in 1966. At the five foot depth, all plant pigment groups were two to three times higher in 1967. The mean chlorophyll a concentration at the ten foot depth was thirty per cent higher in 1967 than in 1966, but the other plant pigment concentrations were not significantly different at that depth. At the remaining depths (15, 20 and 35 feet), chlorophylls a, b and c, and non-astacin carotenoids occurred in approximately the same concentrations in 1967 as in 1966. Although the mean concentration of astacin carotenoids was low for both summers, the averages for

1966 were somewhat higher than those for 1967 at all depths except 2.5 feet, where the values were identical. The pigment concentration values of 1967 are considered to be more accurate than those obtained in 1966, because a correction was made for turbidity in the acetone-pigment solutions. This correction was accomplished by subtracting the absorbance reading at 750 millimicrons, a wavelength at which none of the pigments absorbs any light, from the absorbance values at 480, 510, 630, 645 and 665 millimicrons, before these readings are used for calculation of pigment concentrations.

As in 1966, the pigment concentrations calculated on an area basis do not directly reflect the amount of periphyton growth at each depth in the bay. This point is illustrated by the relationship between total chlorophyll and ash-free dry weight of periphyton at the standard depths (see Figure 82). The amount of total chlorophyll rose from 5.58×10^{-3} milligrams per milligram of ash-free dry weight at 2.5 feet to 8.14×10^{-3} milligrams per milligram of ash-free dry weight at thirty-five feet. The major increase in concentration occurred between the fifteen and twenty foot depths (6.12×10^{-3} mg. chlorophyll/mg. ash-free dry weight to 7.85×10^{-3} mg. chlorophyll/mg. ash-free dry weight). The relationship between chlorophyll concentration and biomass is further established by consideration of the total numbers of organisms at each depth. A continuous downward trend in the counts as depth increased was obvious. The organisms in deeper water apparently had increased their pigment concentrations in response to lower light intensity as in 1966. However, the relationship between total chlorophyll and ash-free dry weight (Figure 82) indicates that this increase was not so marked in 1967 as the pigment per organism ratios of 1966 would suggest.

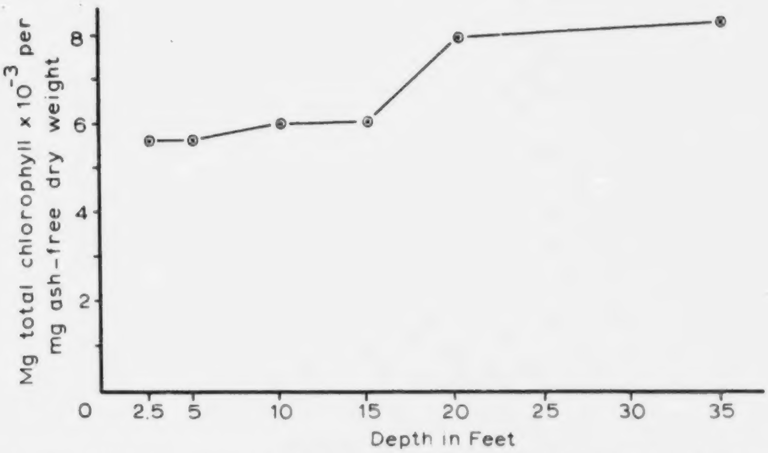

Figure 82. Average Periphyton Total Chlorophyll Concentration (per unit ash-free dry weight) at Standard Sampling Depths, Stony Point Bay, Lake Superior, 1967.

The increased periphyton biomass in the shallow water of Stony Point Bay in 1967 (indicated by pigment concentrations) may be explained on the basis of weather. Very few violent storms arose during the summer of 1967; the organisms growing in the shallow waters were disturbed less often by currents and wave action than in 1966. East and northeast winds cause the most severe turbulence along the north shore of Lake Superior because their course parallels the long axis of the lake. United States Department of Commerce local climatological data show that no northeast winds occurred in the general area during the 1967 sampling period. East winds occurred on only eleven of the sixty-seven days, or sixteen per cent of the time. During the summer of 1966, east and northeast winds prevailed thirty-nine per cent of the time. These data reinforce personal observations which indicated that the waters of Stony Point Bay were much calmer during the 1967 season than in 1966. The hypothesis is that many periphytic organisms were washed away from the shallow areas in 1966, while those in relatively deep water were not affected by wave action. Thus the biomass in deep water was of approximately the same magnitude both summers.

The variations in pigment concentrations at each depth (on a unit area basis) according to sampling date are presented in Figures 83 through 94. The points represent the individual measurements from which the average concentrations at each depth (Figure 81) were calculated. While the general pattern of Figure 81 may be seen by superimposing the individual graphs and observing the area under each curve, it is obvious that the variation in terms of time is not the same at each depth. In discussing these variations, the sample taken on November 10 will be considered separately.

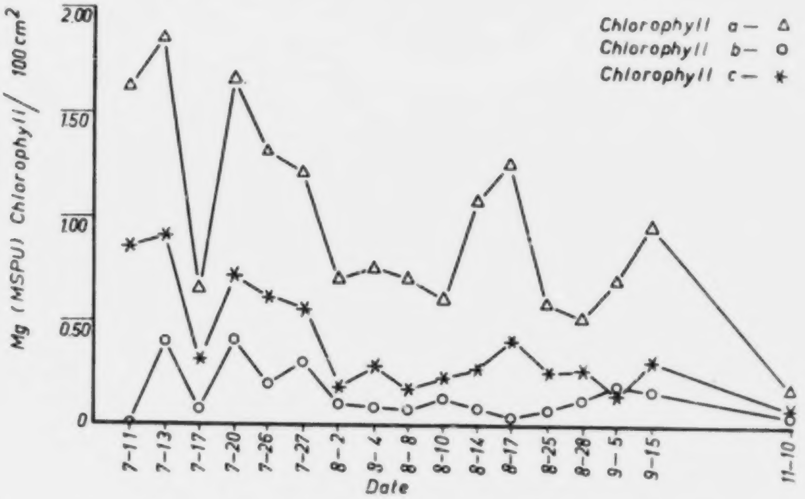

Figure 83. Periphyton Chlorophyll Concentrations (per unit area) at 2.5 feet, Stony Point Bay, Lake Superior, 1967.

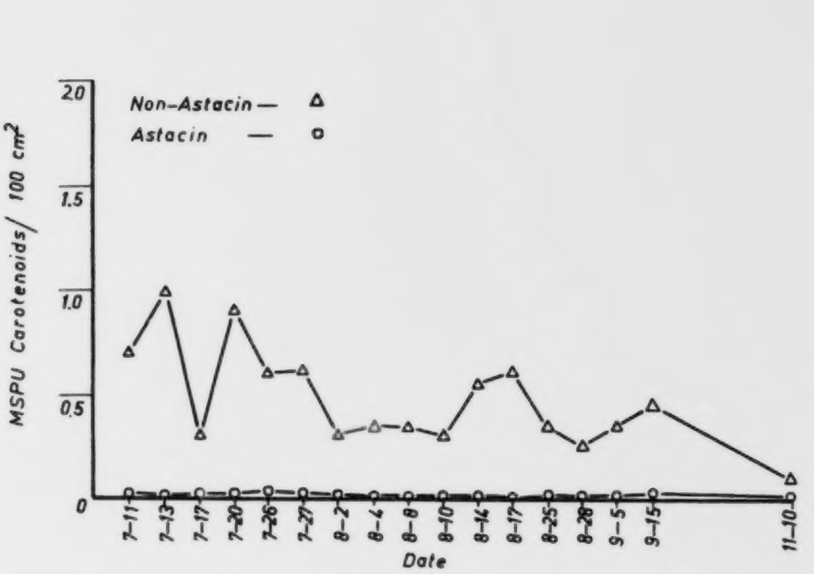

Figure 84. Periphyton Carotenoid Concentrations (per unit area) at 2.5 Feet, Stony Point Bay, Lake Superior, 1967.

At the 2.5 foot depth (Figures 83 and 84) the maximum concentrations of all five pigment groups occurred early in the season; all of the pigments peaked on July 13, except the astacin carotenoids, which were highest on the first sampling day (July 11). The minimum values for each pigment type at 2.5 feet were obtained near the end of August. The maximum concentrations were about three times as high as the minimum concentrations. For example, the maximum chlorophyll a value was 1.863 milligrams per 100 square centimeters on July 13, while the minimum was 0.547 milligrams per 100 square centimeters on August 28. While major peaks in the curves appeared on July 20, August 17 and September 15, the general downward trend of each of the pigment groups during the season is apparent.

There is no suggestion of a downward trend in pigment concentrations during the summer at the five foot depth (see Figures 85 and 86). The concentration of total pigments per unit area remained rather constant throughout the sampling period. The maximum concentration of chlorophyll a (0.930 mg./100 cm^2) and non-astacin carotenoids (0.465 MSPU/100 cm^2) occurred on July 27. Slightly lower peaks appeared on August 10 and 28. The concentrations of chlorophylls b, c, and astacin carotenoids reached their highest levels on August 28. The most obvious depression in the major plant pigment curves occurred on August 4.

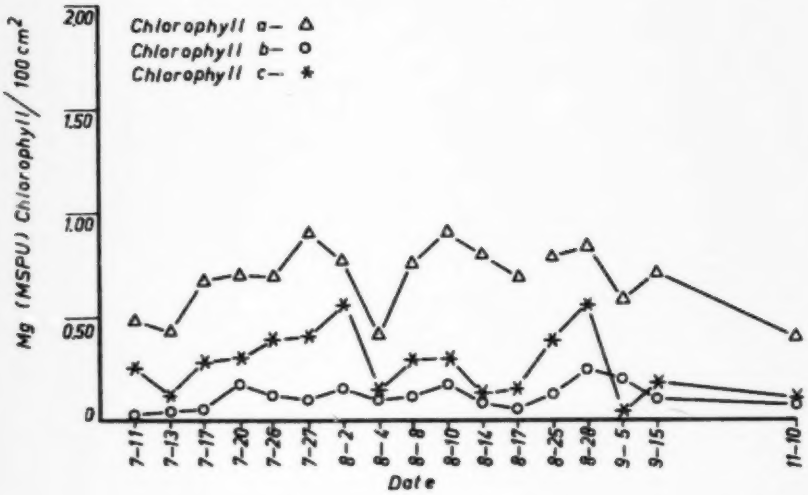

Figure 85. Periphyton Chlorophyll Concentrations (per unit area) at Five Feet, Stony Point Bay, Lake Superior, 1967.

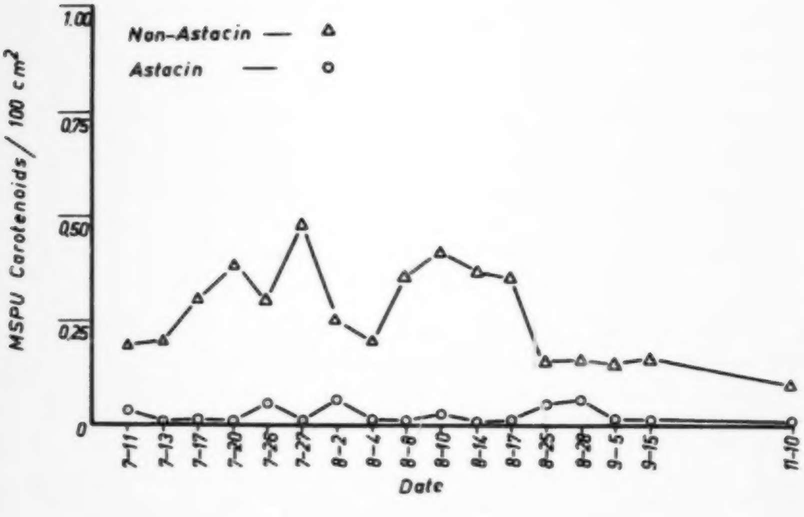

Figure 86. Periphyton Carotenoid Concentrations (per unit area) at Five Feet, Stony Point Bay, Lake Superior, 1967.

Two major peaks were observed in the concentrations of all the periphyton pigments in samples from a depth of ten feet (Figures 87 and 88). The maximum values for chlorophyll a (1.102 mg./100 cm^2), chlorophyll c (0.472 MSPU/100 cm^2), and non-astacin carotenoids (0.463 MSPU per 100 cm^2) occurred on August 2. Chlorophyll b and astacin carotenoid concentrations were highest on August 25. Between these two dates, the level of all the pigment groups remained quite low. No general trend during the sampling period is apparent.

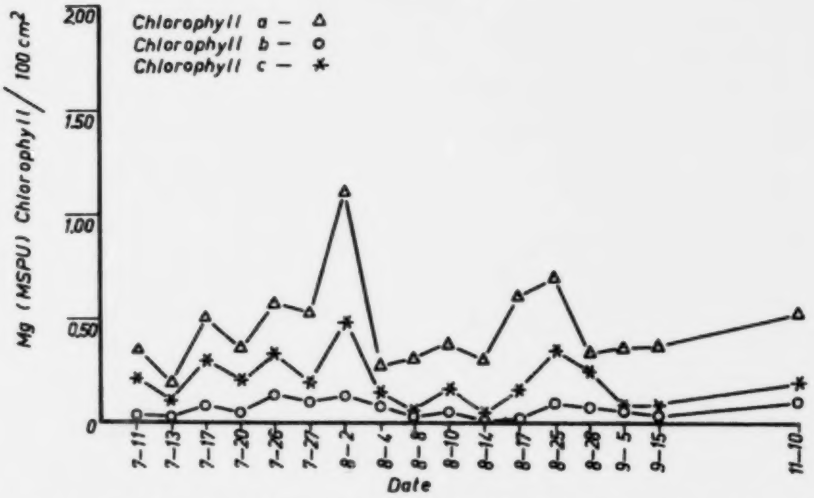

Figure 87. Periphyton Chlorophyll Concentrations (per unit area) at Ten Feet, Stony Point Bay, Lake Superior, 1967.

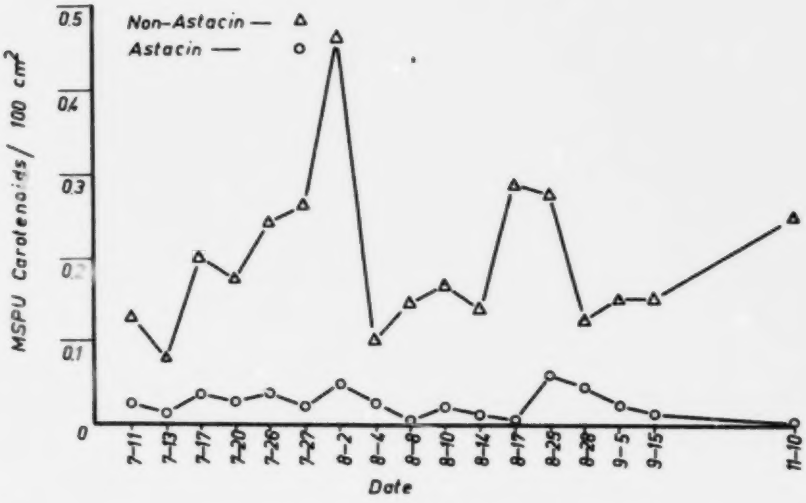

Figure 88. Periphyton Carotenoid Concentrations (per unit area) at Ten Feet, Stony Point Bay, Lake Superior, 1967.

The pigment concentrations at fifteen feet were lower and less variable than at all other depths during most of the summer (Figures 89 and 90). The chlorophyll a curve includes two peaks of nearly equal magnitude (0.468 mg. per 100 cm^2 on July 27, and 0.490 mg./100 cm^2 on August 17). The non-astacin carotenoid values show a very similar pattern, peaking on the same two days. Chlorophyll c, however, peaked on July 20, while chlorophyll b reached its maximum level on August 28. The concentrations of all the pigment types were lowest in September.

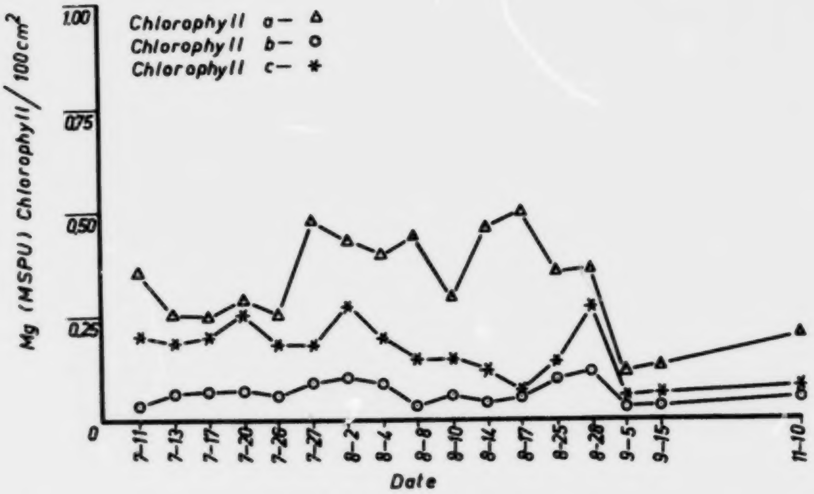

Figure 89. Periphyton Chlorophyll Concentrations (per unit area) at Fifteen Feet, Stony Point Bay, Lake Superior, 1967.

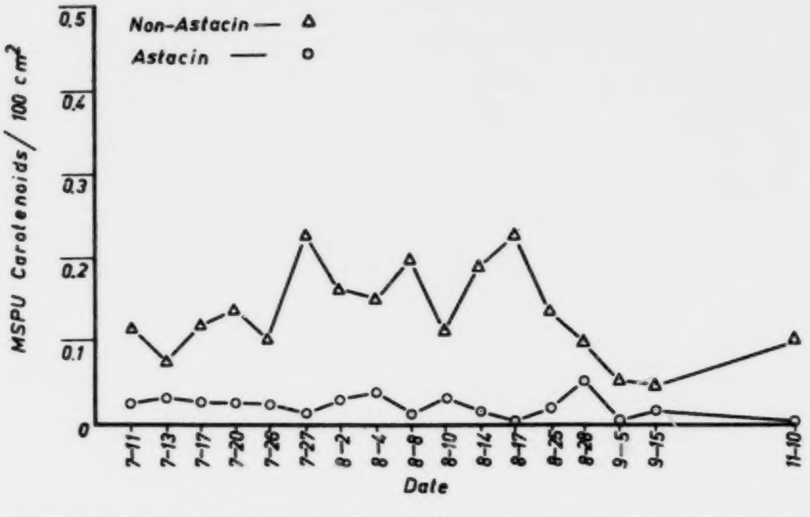

Figure 90. Periphyton Carotenoid Concentrations (per unit area) at Fifteen Feet, Stony Point Bay, Lake Superior, 1967.

Figures 91 and 92 show that the periphyton pigments generally increased on a unit area basis at a depth of twenty feet during the sampling period. Chlorophyll a rose from 0.201 milligrams per 100 square centimeters on July 11 to a maximum of 0.784 milligrams per 100 square centimeters on August 25. In similar fashion, the non-astacin carotenoid level increased from 0.036 MSPU per 100 square centimeters on July 11 to 0.319 MSPU per 100 square centimeters on Septebmer 5. The maximum chlorophyll c value (0.473 MSPU/100 cm^2) appeared on August 25, as did the highest chlorophyll b level (0.142 mg./100 cm^2). The major pigments underwent a series of continuous increases and decreases between August 10 and September 15.

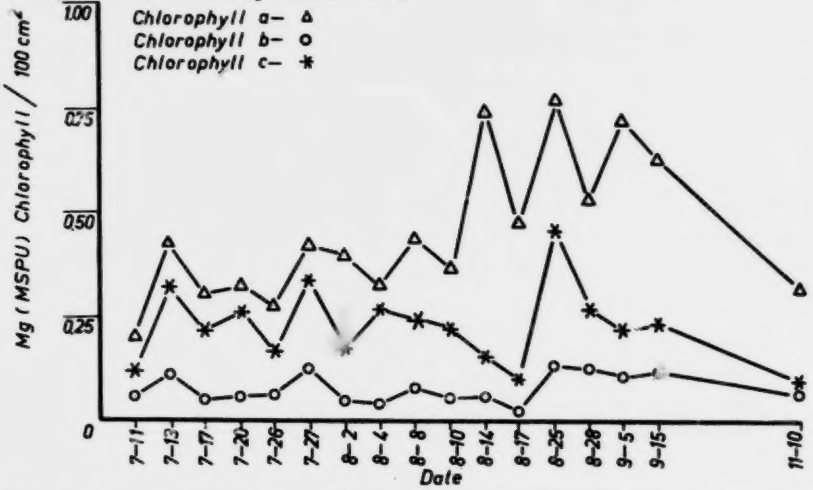

Figure 91. Periphyton Chlorophyll Concentrations (per unit area) at Twenty Feet, Stony Point Bay, Lake Superior, 1967.

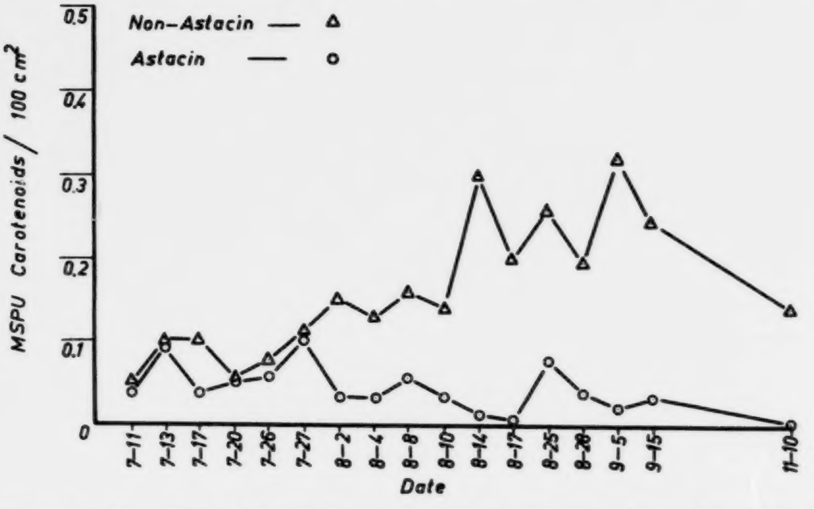

Figure 92. Periphyton Carotenoid Concentrations (per unit area) at Twenty Feet, Stony Point Bay, Lake Superior, 1967.

The pigment concentrations at thirty-five feet also exhibited a general increase during the summer (see Figures 93 and 94). The minimum chlorophyll a value, 0.303 mg./100 cm^2, occurred on July 17 and the maximum, 1.046 mg./100 cm.^{2}, on September 5. Chlorophylls b, c, and non-astacin carotenoids reached their highest levels on September 5 or 15. The seasonal rise in the major pigment concentrations was generally smooth, the only apparent depression occurring on August 28. The astacin carotenoid values for the thirty-five foot samples, as for those from all other depths, remained very low and varied little during the sampling period.

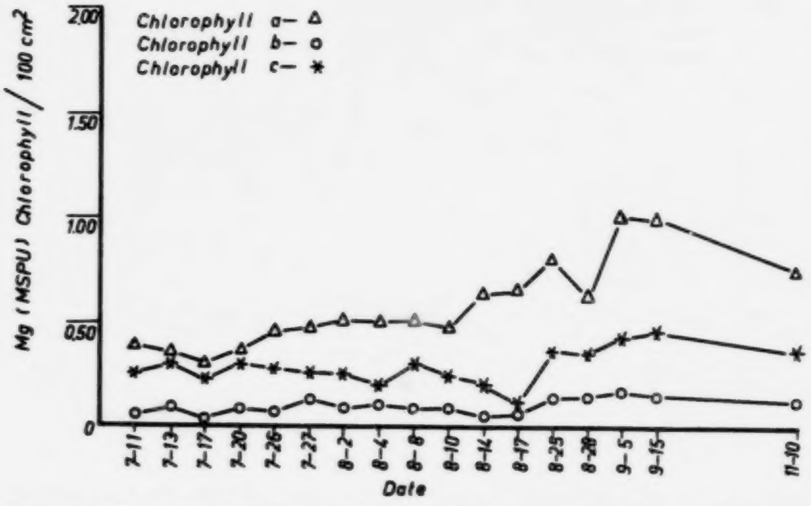

Figure 93. Periphyton Chlorophyll Concentrations (per unit area) at Thirty-Five Feet, Stony Point Bay, Lake Superior, 1967.

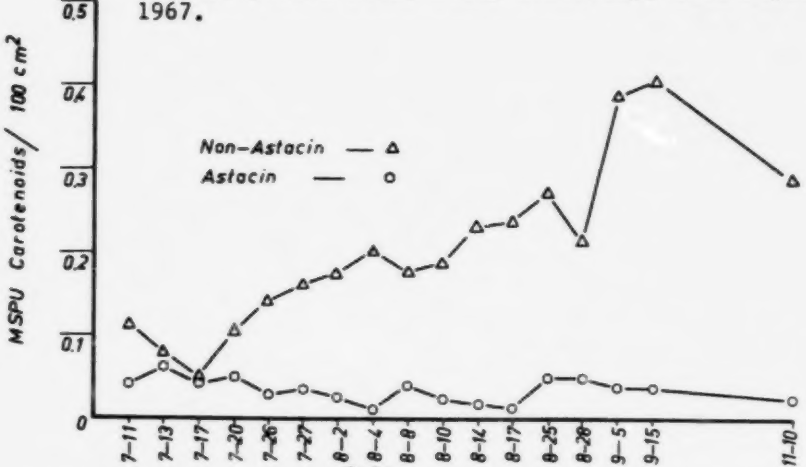

Figure 94. Periphyton Carotenoid Concentrations (per unit area) at Thirty-Five Feet, Stony Point Bay, Lake Superior, 1967.

It is not possible to account for each rise and fall in the pigment concentrations at the various depths throughout the summer. However, there are reasonable explanations for differences between the trends exhibited by the pigment concentrations at various depths, and for some decreased in concentration on specific days. The rather large variation in pigment concentrations at the shallower depths (2.5 to 10 feet) during the sampling period probably reflects the action of waves on the periphyton. The depressions and peaks represent removal of organisms as a result of turbulent water and subsequent regrowth during relatively calm periods. However, the high mean pigment concentrations in the shallow water indicate that the biomass in these areas was never seriously reduced by wave action. Some of the variability in biomass in shallow water may also have been due to a relatively lesser degree of homogeneity in the community in terms of area than in deeper water. The continual rise in pigment concentrations at the twenty and thirty-five foot depths during the summer is probably indicative of a true seasonal increase in biomass, which reached a maximum on September 5. Presumably, the turbulence in shallow water was more severe than that occurring elsewhere, and sufficient strength to disturb the periphyton organisms. However, the depression in pigment concentrations on August 28 at all depths indicates that a current affecting all parts of the sampling area developed between August 25 and 28. Such a current might be produced by strong, shifting local winds. Weather data show that rainstorms and winds in excess of twenty-five miles per hour occurred in the sampling area on August 26 and 27. During this period, the winds shifted from south to northwest, and probably produced enough water movement to remove part of the periphyton at all depths in the bay.

Analysis of samples collected on November 10 revealed that the pigment concentrations on a unit area basis had decreased considerably at all depths except ten and fifteen feet, where the concentrations were never particularly high. The highest concentration of pigments was present at a depth of thirty-five feet, while the lowest concentration was encountered at 2.5 feet. For example, chlorophyll a ranged from 0.165 milligrams per 100 square centimeters at 2.5 feet to 0.752 milligrams per 100 square centimeters at thirty-five feet. Part of the general decrease in pigment concentrations between September 15 and November 10 may have been due to seasonal reduction in growth; however, since the pigment concentrations were highest at thirty-five feet, it is more likely that a severe storm removed much of the periphyton from the rocks in the shallow water.

The foregoing explanations regarding the variations in pigment concentrations during the summer are valid only if the pigment values are correlated well enough with the numbers of organisms to indicate the general magnitude of biomass at each depth. Correlation coefficients were calculated for total counts and total chlorophyll values for samples from each sampling depth. In addition, to facilitate future estimations of numbers of periphyton organisms based on total chlorophyll concentration, regression lines were constructed using the least squares method. Counts (y axis) were plotted against total chlorophyll values (x axis). The regression lines are presented in Figures 95 through 100, along with the correlation coefficients (r), the probability values (P), and the equations for the slope of each line. The procedures followed in the calculation of correlations and regressions are described in Appendix D. The two parameters were found to be positively correlated at all depths, the correlation coefficients (r) ranging from 0.639 (P=0.01) for samples from the 2.5 foot depth to 0.921 (P=0.001) for samples from a depth of thirty-five feet. The correlation was generally better for samples from the deeper water. It should be understood that these rather close correlations do not contradict the findings which show differences in amount of pigment per unit of ash-free dry weight from one depth to another. The correlations and regressions were determined for each depth and do not reflect any differences related to depth. A regression line based on all counts and pigment concentrations irrespective of depth would be useless in light of the fact that different relationships exist between the two values at each depth. However, numbers of organisms in Stony Point Bay may be predicted from total chlorophyll data when the sampling depth is known and the proper regression line is used. The results of such predictions may be expected to be more accurate for samples from deep water than for those from shallow water.

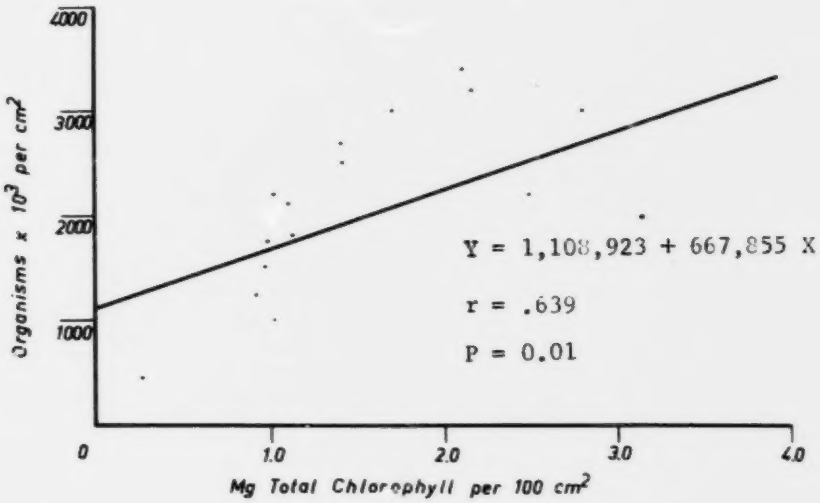

Figure 95. Regression Line, Counts Versus Total Chlorophyll; Naturally Occurring Periphyton at 2.5 Feet, Stony Point Bay, Lake Superior, 1967.

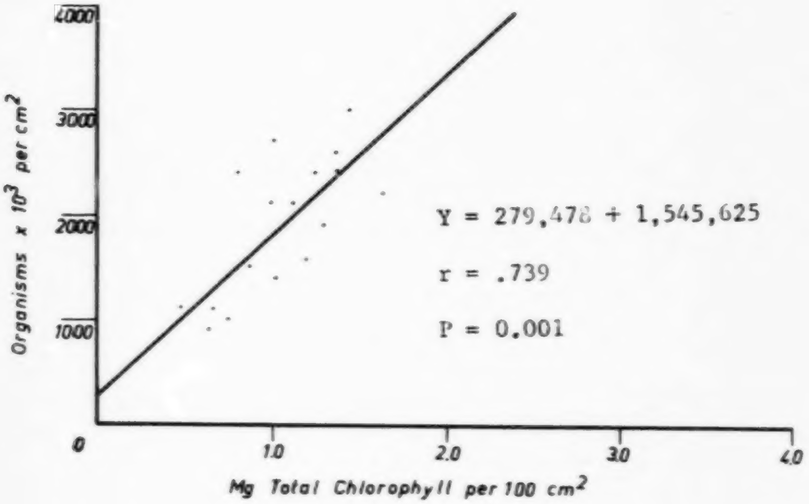

Figure 96. Regression Line, Counts Versus Total Chlorophyll; Naturally Occurring Periphyton at Five Feet, Stony Point Bay, Lake Superior, 1967.

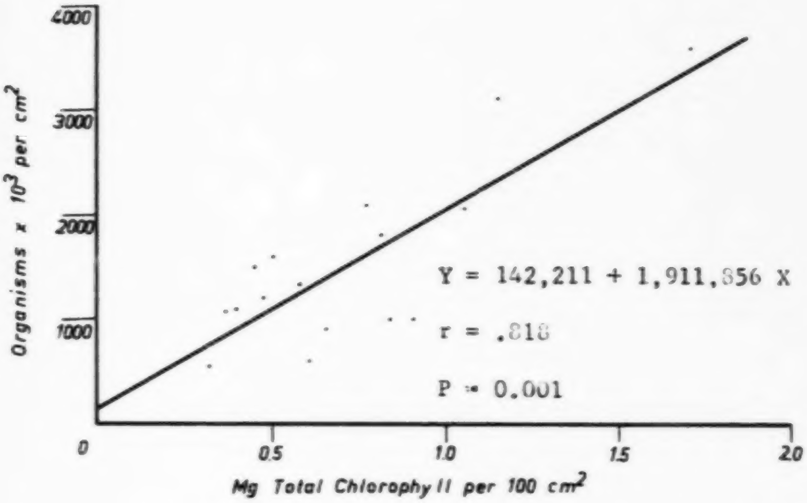

Figure 97. Regression Line, Counts Versus Total Chlorophyll; Naturally Occurring Periphyton at Ten Feet, Stony Point Bay, Lake Superior, 1967.

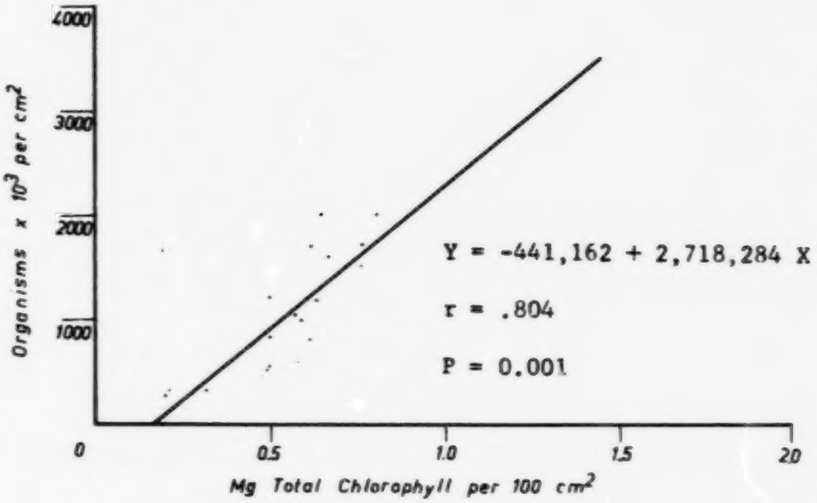

Figure 98. Regression Line, Counts Versus Total Chlorophyll; Naturally Occurring Periphyton at Fifteen Feet, Stony Point Bay, Lake Superior, 1967.

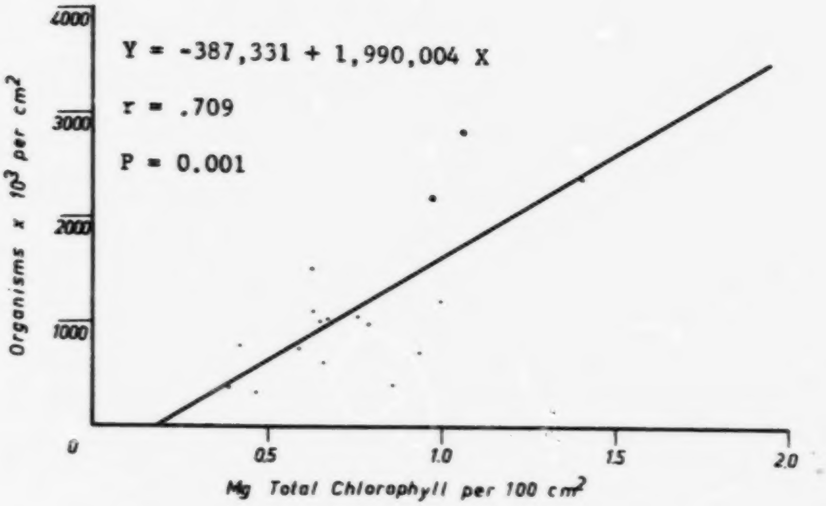

Figure 99. Regression Line, Counts Versus Total Chlorophyll; Naturally Occurring Periphyton at Twenty Feet, Stony Point Bay, Lake Superior, 1967.

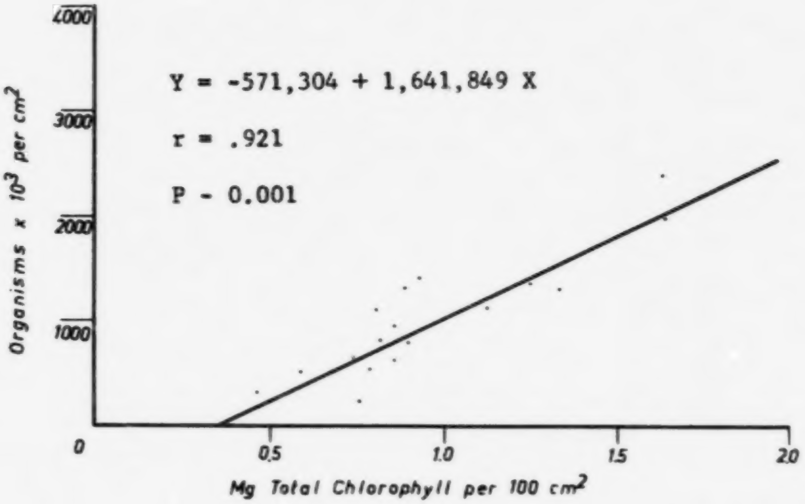

Figure 100. Regression Line, Counts Versus Total Chlorophyll; Naturally Occurring Periphyton at Thirty-Five Feet, Stony Point Bay, Lake Superior, 1967.

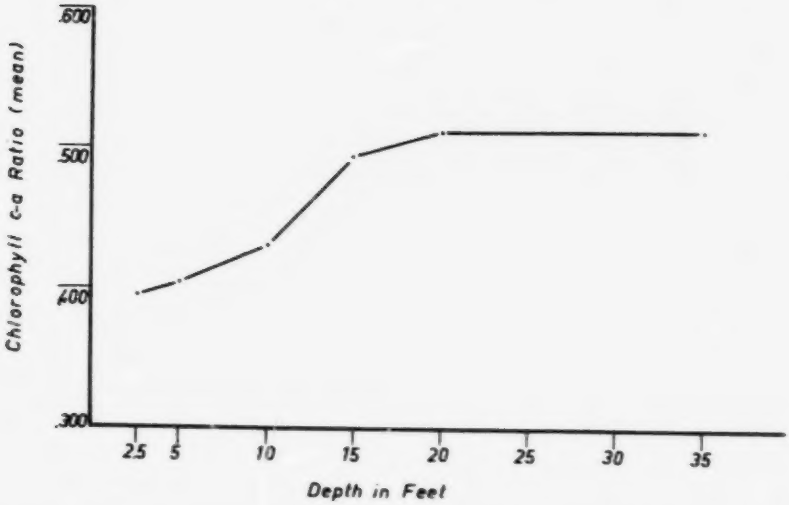

Figure 101. Ratio of Periphyton Chlorophyll c/Chlorophyll a at Standard Sampling Depths, Stony Point Bay, Lake Superior, 1967.

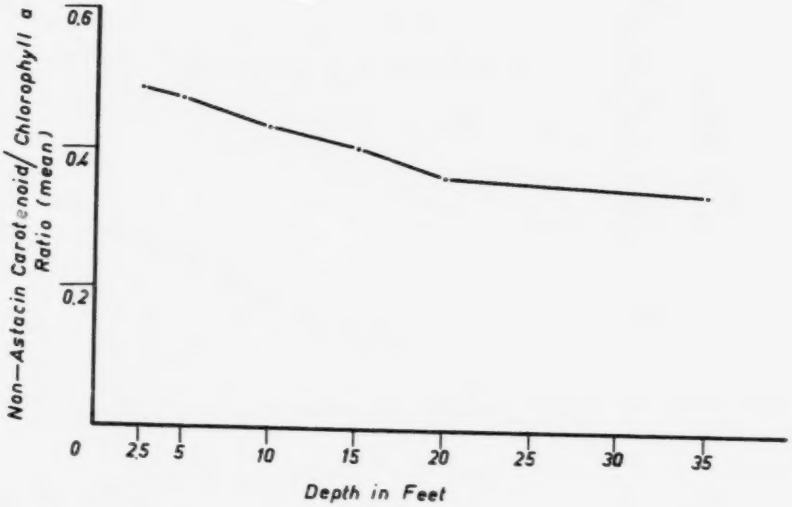

Figure 102. Ratio of Periphyton Non-astacin Carotenoids/Chlorophyll a at Standard Sampling Depths, Stony Point Bay, Lake Superior, 1967.

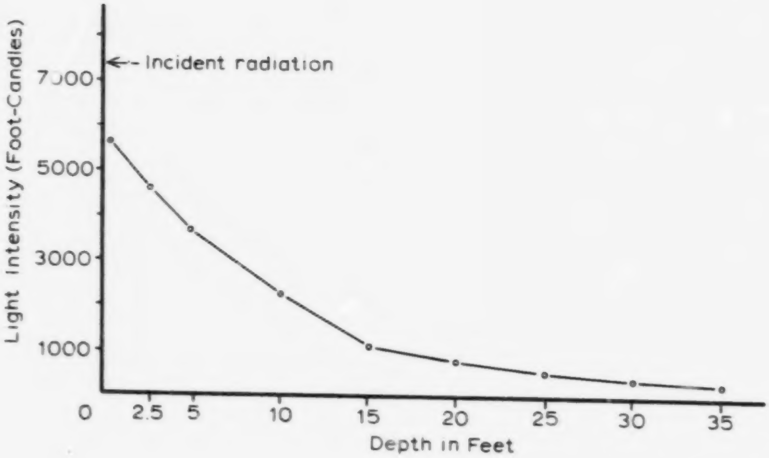

Figure 103. Average Mid-Day Light Intensity at Standard Depths, Stony Point Bay, Lake Superior; June - September, 1967.

The mean ratio of chlorophyll *c*/chlorophyll *a* was 0.459 for the entire bay in 1967. However, the values calculated for each depth range from 0.395 at 2.5 feet to 0.511 at thirty-five feet (see Figure 101). In contrast, the ratio of non-astacin carotenoids/chlorophyll *a* decreased with increasing depth, varying from 0.486 at 2.5 feet to 0.344 at thirty-five feet (Figure 102); the mean for the entire bay was 0.415. The same phenomenon, i.e., a decrease in the ratio of carotenoids/chlorophyll *a* as depth increases, has been reported for stratified marine phytoplankton by Ryther *et al.* (1958). If the species composition of the periphyton were very similar at all depths in the bay, it could be assumed that observed differences in pigment ratios in large samples of the community were a result of differences in the pigment ratios in individual organisms of the same type. It could be further assumed that these differences were due to environmental factors. The species composition of the periphyton community at all depths in Stony Point Bay *was* very constant (Fox, 1969), with diatoms making up over ninety per cent of the population. Percentages of the various types of organisms varied little with depth, so the composition of the community at different depths is not important in explaining varying pigment ratios. With this fact established, other possible reasons for differences in pigment ratios at various depths can be explored. Table XXIII shows that both chlorophyll *a* and chlorophyll *c* increased in relation to ash-free dry weight as depth became greater; however, the amount of chlorophyll *a* per unit of organic weight is increased by only thirty-four per cent from 2.5 feet to thirty-five feet, while chlorophyll *c* is increased by seventy-four per cent. This difference accounts for the rising chlorophyll *c*/*a* ratio as depth is increased. There is virtually no difference in the concentration of non-astacin carotenoids in relation to ash-free dry weight at the standard sampling depths (a decrease of five per cent from 2.5 feet to thirty-five feet). The decreasing ratio of carotenoids/chlorophyll *a* as depth increased is a result only of the rising chlorophyll *a* concentration.

The rise in pigment concentrations in relation to organic weight as depth is increased may be viewed as a response to lower light intensity. The average mid-day light intensity at each sampling depth for 1967 is shown graphically in Figure 103. Each point represents an average of the readings taken on each of the seventeen sampling days.

The average intensity at the surface of the water was 7275 foot-candles. Six inches of water lowered the reading to 5600 foot-candles. From this point the average readings decreased gradually with depth, reaching a minimum of 265 foot-candles at a depth of thirty-five feet. The readings at each depth were quite variable, depending on atmospheric conditions and the effects of turbidity on the day a measurement was made. It has been shown that visible light of relatively short wavelength penetrates deeper into pure water than light of longer wavelength; the same phenomenon, with certain variations, occurs in water containing dissolved and suspended solids (Clarke, 1954). Since the major absorption peak in the red band for chlorophyll *c* is at a lower wavelength than the peak for chlorophyll a, the preferential increase in chlorophyll c by the periphyton as light intensity decreases may be a response to the greater proportion of shorter wavelength light in deep water.

TABLE XXIII

PERIPHYTON PIGMENT CONCENTRATIONS IN RELATION TO
ASH-FREE DRY WEIGHT AT STANDARD DEPTHS,
STONY POINT BAY, LAKE SUPERIOR, 1967

	Mg pigment x 10^{-3}/mg ash-free dry weight		
Depth	Chlorophyll a	Chlorophyll c	Non-astacin carotenoids
2.5 ft.	3.62	1.42	1.76
5	3.50	1.43	1.64
10	3.79	1.64	1.65
15	3.64	1.79	1.45
20	4.65	1.94	1.64
35	4.86	2.48	1.67

TABLE XXIV

SEASONAL VARIATION OF PERIPHYTON PIGMENT RATIOS
STONY POINT BAY, LAKE SUPERIOR, 1967
(ALL DEPTHS COMBINED)

Date	$\frac{\text{Chlorophyll c}}{\text{Chlorophyll a}}$	$\frac{\text{Chlorophyll b}}{\text{Chlorophyll a}}$	$\frac{\text{Non-astacin carotenoids}}{\text{Chlorophyll a}}$
7-11	.588	.115	.348
7-13	.611	.208	.364
7-17	.636	.163	.372
7-20	.677	.222	.408
7-26	.591	.195	.324
7-27	.511	.214	.428
8-2	.522	.171	.391
8-4	.510	.190	.417
8-8	.384	.129	.428
8-10	.460	.181	.431
8-14	.227	.072	.424
8-17	.242	.059	.453
8-25	.464	.160	.383
8-28	.622	.263	.383
9-5	.284	.224	.452
9-15	.342	.164	.418

In order to determine whether or not the various pigment ratios changed during the season, the ratios were calculated on the basis of combined pigment concentrations from all depths for each sampling day. The ratios of chlorophyll c, chlorophyll b, and non-astacin carotenoids, respectively, to chlorophyll a for each day are presented in Table XXIV. The chlorophyll c/a ratios exhibit considerable variation, but no seasonal trend is apparent. The ratio of non-astacin carotenoids to chlorophyll a is quite constant; a slight upward trend during the summer is indicated. It is reasonable that the chlorophyll c/a ratio was much more erratic on a seasonal basis than the carotenoid/chlorophyll a ratio, since the concentration of chlorophyll c seems to be subject to control by the intensity or spectral composition of light. The changes in the c/a ratio during the sampling period may be indicative of variable light intensity due to turbidity. The ratios of chlorophyll b to chlorophyll a, which should reflect the relative numbers of green algae present in the samples, are quite variable and show no particular trend. The highest ratio occurred on August 28 and the lowest on August 17.

The dry weights and ash-free dry weights of all periphyton samples collected from Stony Point Bay in 1967 are presented in Tables XXV and XXVI. The seasonal variation of the ash-free dry weights at each sampling depth is shown graphically in Figures 104 through 109. Each weight may be compared directly to a corresponding pigment concentration, since samples for both determinations were taken from the same periphyton suspension. The mean dry weight per unit area of rock surface was highest for samples from a depth of 2.5 feet and lowest for those from thirty-five feet (Table XXV). The dry weights decreased with increasing depth, except between fifteen and twenty feet, where the average weights were nearly identical. The highest mean ash-free dry weight, 2.7 milligrams per square centimeter occurred at 2.5 feet, while the lowest, 0.91 milligrams per square centimeter, was recorded at fifteen feet (Table XXVI). The weights increased slightly from fifteen to thirty-five feet. The ash-free dry weights of the 1967 samples were found to be well correlated with total counts of organisms. However, as shown by Figure 82, the relationship between the organic weights and pigment concentration was not constant at all depths.

TABLE XXV

NATURALLY OCCURRING PERIPHYTON DRY WEIGHTS AT THE STANDARD SAMPLING DEPTHS
STONY POINT BAY, LAKE SUPERIOR, 1967
MILLIGRAMS PER SQUARE CENTIMETER OF ROCK SURFACE

Date	Sampling depth in feet					
	2.5	5	10	15	20	35
7-11	28.8	7.4	9.0	7.8	3.3	6.0
7-13	30.0	8.7	4.4	6.2	9.2	7.9
7-17	19.7	26.1	9.6	6.1	7.4	- *
7-20	33.3	10.7	10.5	10.8	4.7	8.1
7-26	39.8	18.4	16.5	14.5	8.1	8.4
7-27	38.9	17.2	17.7	15.2	7.2	7.3
8-2	28.9	14.4	16.2	17.6	8.5	11.0
8-4	14.8	5.9	12.7	18.8	13.8	9.0
8-8	21.2	19.8	10.4	11.3	27.8	10.5
8-10	12.5	20.3	9.0	10.6	11.5	10.4
8-14	27.9	11.7	9.2	16.7	15.8	10.9
8-17	21.4	13.6	14.3	17.9	12.1	10.5
8-25	21.9	36.0	44.3	14.0	20.3	13.9
8-28	23.3	29.6	10.5	14.8	9.3	13.6
9-5	52.0	21.5	12.1	4.8	13.7	19.6
9-15	39.5	28.8	10.7	3.1	17.5	17.2
11-10	21.3	21.3	17.5	13.4	17.0	13.8
Mean	27.9	18.2	13.8	11.9	12.1	10.4

* Sample was lost

TABLE XXVI

NATURALLY OCCURRING PERIPHYTON ASH-FREE DRY WEIGHTS AT THE STANDARD SAMPLING DEPTHS STONY POINT BAY, LAKE SUPERIOR, 1967 MILLIGRAMS PER SQUARE CENTIMETER OF ROCK SURFACE

Date	Sampling depth in feet					
	2.5	5	10	15	20	35
7-11	3.63	1.37	1.23	1.02	0.64	1.14
7-13	2.53	1.62	0.58	0.63	0.63	0.63
7-17	1.90	1.75	0.98	0.46	0.84	-*
7-20	2.90	1.80	1.03	0.85	0.47	0.69
7-26	3.39	2.04	2.00	1.22	1.05	1.05
7-27	3.95	3.04	1.38	1.11	0.30	0.96
8-2	2.46	1.96	2.07	1.29	0.97	1.04
8-4	2.88	1.10	1.12	1.22	0.97	1.09
8-8	2.09	1.70	1.19	1.10	1.97	1.58
8-10	2.43	2.28	0.71	0.55	0.72	0.80
8-14	2.77	1.46	0.52	0.93	1.08	0.82
8-17	2.66	1.28	1.01	0.77	0.72	1.61
8-25	2.58	2.32	2.25	1.01	1.66	1.18
8-28	2.72	2.27	1.38	1.81	1.04	1.48
9-5	3.86	1.72	1.50	0.88	1.82	2.32
9-15	2.96	2.78	0.81	0.33	1.25	1.65
11-10	0.33	1.13	0.85	0.44	0.55	1.17
Mean	2.70	1.92	1.21	0.91	0.98	1.20

*Sample was lost

The following figures (104-109) present the detailed information relative to seasonal variations in ash-free dry weights, and as indicated earlier each weight may be compared directly to a corresponding pigment concentration inasmuch as samples for both determinations were taken from the same periphyton suspension.

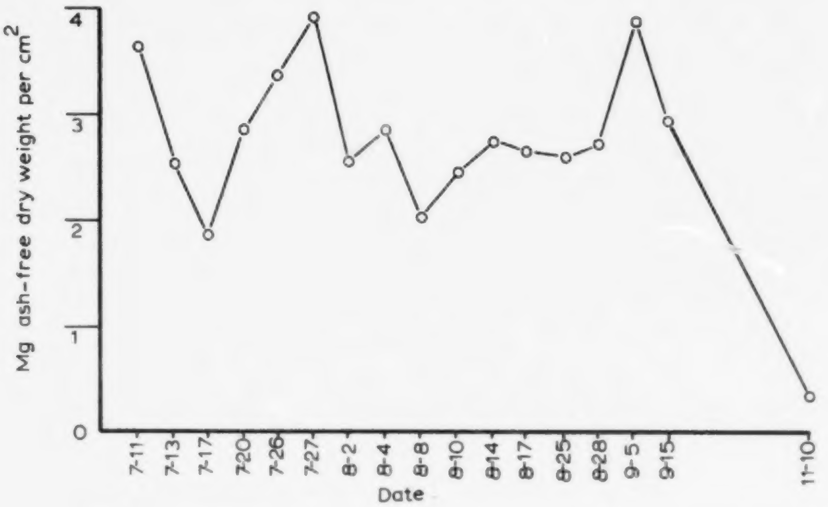

Figure 104. Periphyton Ash-Free Dry Weights (per unit area) at 2.5 Feet, Stony Point Bay, Lake Superior, 1967.

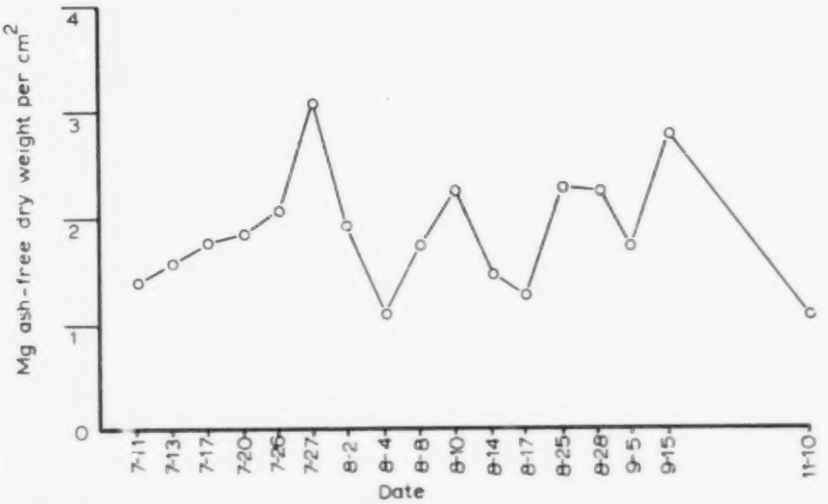

Figure 105. Periphyton Ash-Free Dry Weights (per unit area) at Five Feet, Stony Point Bay, Lake Superior, 1967.

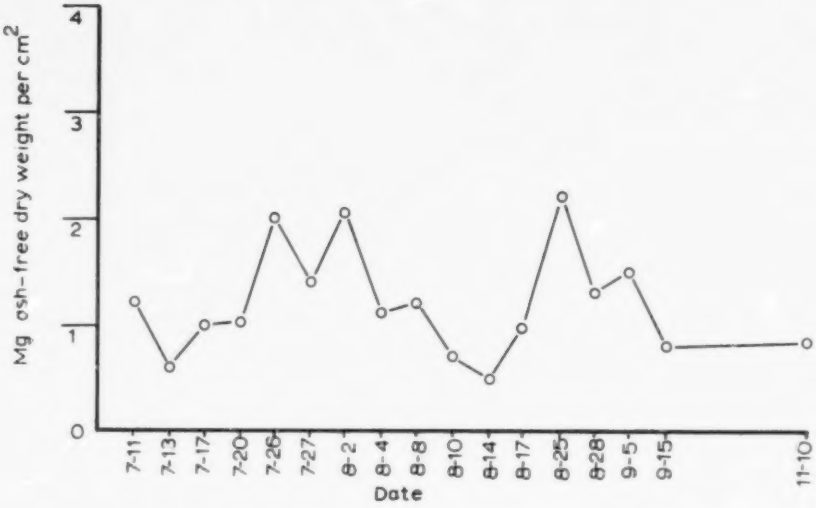

Figure 106. Periphyton Ash-Free Dry Weights (per unit area) at Ten Feet, Stony Point Bay, Lake Superior, 1967.

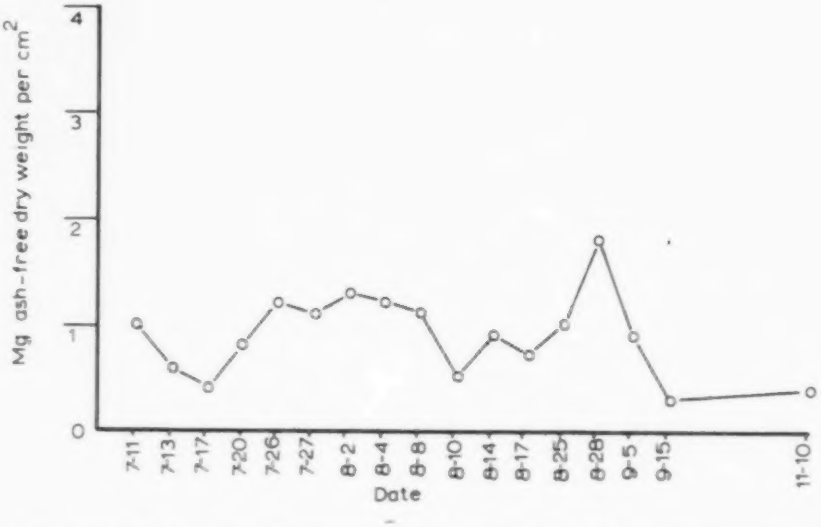

Figure 107. Periphyton Ash-Free Dry Weights (per unit area) at Fifteen Feet, Stony Point Bay, Lake Superior, 1967.

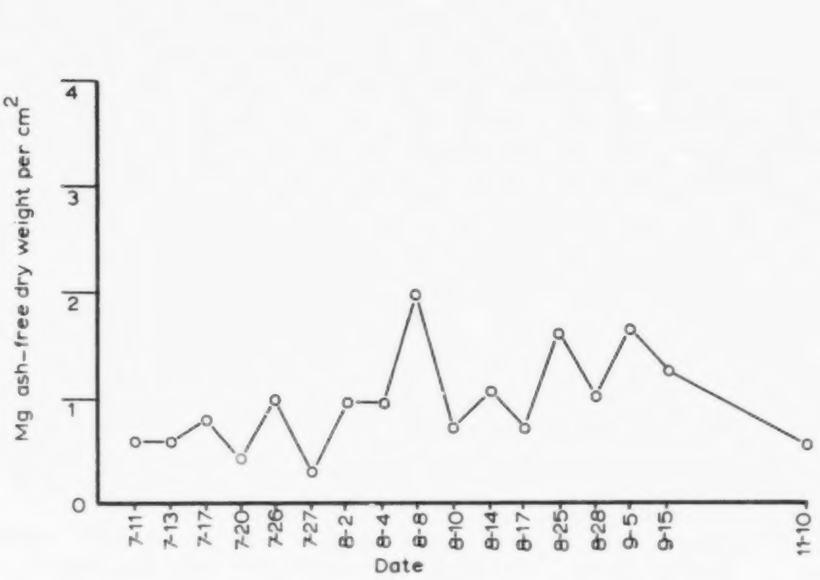

Figure 108. Periphyton Ash-Free Dry Weights (per unit area) at Twenty Feet, Stony Point Bay, Lake Superior, 1967.

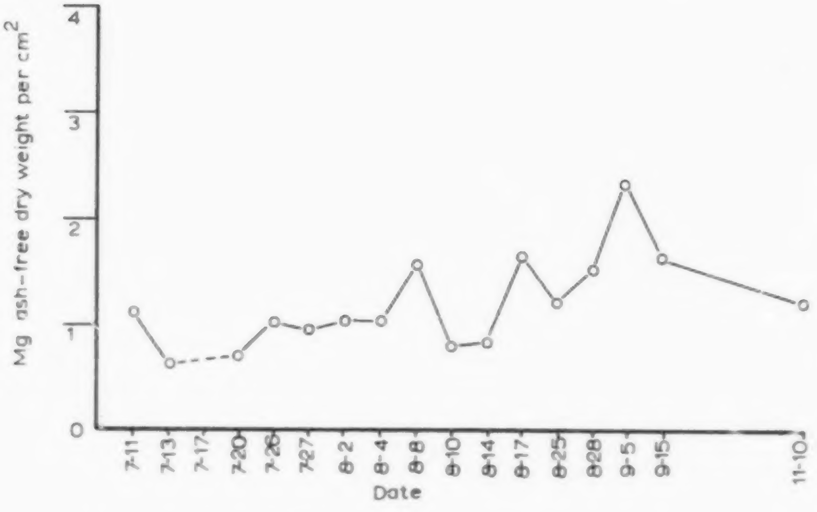

Figure 109. Periphyton Ash-Free Dry Weights (per unit area) at Thirty-Five Feet, Stony Point Bay, Lake Superior, 1967.

On the basis of the average dry weight of all samples taken during 1967, the total dry weight of the periphyton in Stony Point Bay was calculated to be 55.5 tons (156 grams per square meter). The corresponding ash-free dry weight was 4.4 tons (12 grams per square meter), or 7.9 per cent of the total dry weight. The mild weather of 1967 was probably the main reason why the total dry weight (55.5 tons) was higher than that produced in 1966 (37.1 tons). Since the 1966 samples seemed to contain more sand and clay than the 1967 samples, the actual difference in weight may have been somewhat greater.

It has been suggested that low temperature may be part of the reason for less extensive growths of periphyton in the deeper water of Stony Point Bay. Temperature data for 1967 show that the deeper water was in fact colder than the shallow water (see Table XXVII). Water temperatures were taken each sampling day at every sampling depth as well as at a point just below the surface of the water. It is obvious that the water temperatures decreased with increasing depth throughout the summer. The values at 2.5 feet ranged from 6.5° C. to 19.5° C. The minimum and maximum temperatures were slightly lower at each depth from five feet to twenty feet. The biggest difference was usually between twenty and thirty-five feet. The temperatures at all depths increased continually during the first two-thirds of the sampling period, reading a maximum on August 14. After that date, the temperatures tended to decrease slightly at all depths except twenty and thirty-five feet. At the twenty foot depth, the maximum temperature, 14.0° C., was recorded on August 14, and again on September 15. The thirty-five foot maximum, 9.5° C., occurred on August 14, 25, 28, and September 5. Even at these times, the temperatures at 2.5, 5, and 10 feet were about twice as high as the thirty-five foot value. On November 10, the temperatures at all depths in the bay were very similar to those recorded on the first day of the sampling period, July 11.

The average gross photosynthetic rate of periphyton organisms taken from each depth in Stony Point Bay is presented in Figure 110. The values are reported in terms of microliters of oxygen evolved per hour per square centimeter of rock surface and were determined manometrically at 20° C. and at a light intensity of 1500 foot-candles. Samples from 2.5 feet produced the highest mean rate of oxygen evolution (44.6 microliters per hour per square centimeter). Samples from each successive depth evolved less oxygen per hour than the preceding ones, except the twenty foot samples, which produced slightly more than the fifteen foot samples. The mean production rate for the samples from thirty-five feet was only 15.3 microliters of oxygen per hour per square centimeter. The 1967 values were lower than those recorded for Stony Point Bay in 1966. This difference probably occurred because no carbon dioxide was added to the atmosphere above the reaction flasks in the respirometer. None was added because it seemed to slow the equilibration of gas phases in the system rather than to speed the process. It was difficult also, to add the gas mixture without pressurizing the system. The introduction of normal atmospheric air to the gas spaces above the samples probably produced more accurate readings.

TABLE XXVII

TEMPERATURES AT THE STANDARD DEPTHS
STONY POINT BAY, LAKE SUPERIOR, 1967
DEGREES CENTIGRADE

	Depth in Feet						
Date	Surface	2.5	5	10	15	20	35
7-11	6.5	6.5	6.0	5.5	5.5	5.0	4.5
7-13	6.0	6.0	6.0	6.0	5.0	4.5	4.5
7-17	6.5	6.5	6.5	6.5	5.5	5.5	5.0
7-20	7.5	7.5	7.0	7.0	6.0	5.5	5.0
7-26	8.0	8.0	7.5	6.5	5.5	5.0	5.0
7-27	9.5	9.5	9.0	7.5	6.0	5.0	5.0
8-2	11.0	10.5	10.5	10.5	9.5	6.5	5.5
8-4	12.5	12.5	12.5	12.0	10.0	8.0	7.0
8-8	16.5	16.0	15.0	15.0	15.0	10.0	8.5
8-10	18.0	18.0	17.5	15.0	14.5	13.5	9.5
8-14	19.5	19.5	19.0	17.5	16.0	14.0	9.5
8-17	17.7	17.0	17.0	16.0	14.0	11.0	8.5
8-25	16.5	16.0	15.5	15.5	12.0	11.0	9.5
8-28	15.5	15.5	15.5	15.0	13.5	12.5	[illegible]
9-5	16.0	15.5	15.0	15.0	14.0	13.5	9.5
9-15	15.5	15.0	14.5	14.5	14.5	14.0	7.0
11-10	7.5	6.5	5.5	5.0	4.5	4.5	4.5

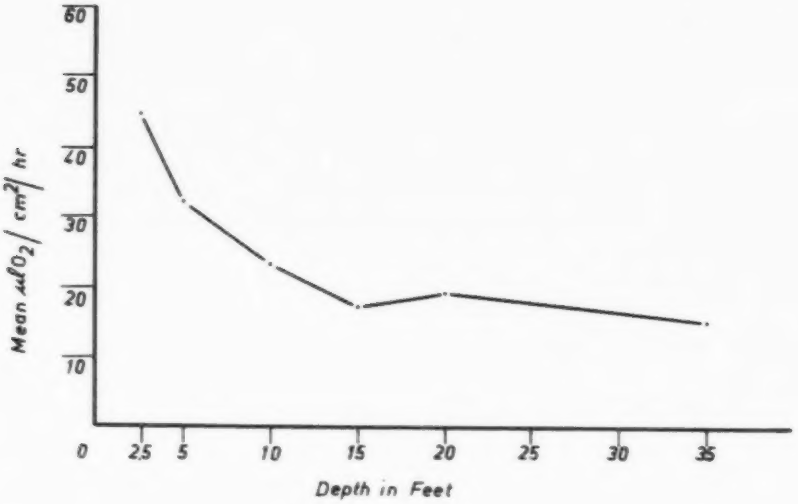

Figure 110. Average Periphyton Gross Photosynthetic Rates (per unit area) for Samples from Standard Depths,[1/] Stony Point Bay, Lake Superior, 1967; Run at 20° C., 1500 Foot-Candles.

The variation in oxygen production by the periphyton samples from each depth during the entire summer may be seen in Figures 111 through 116. While the total amount of pigment per unit area seemed to decrease during the season at the 2.5 foot depth, the amount of oxygen produced tends to increase with time. After an initial reading of 58.4 microliters of oxygen per hour per square centimeter on July 11, the rate dropped to 15.6 microliters/hour/cm^2 on July 17 before rising eventually to the maximum value of 70.6 microliters/hour/cm^2 on August 25 (see Figure 111). Gross photosynthesis also increased during the summer at all the other depths, even though the counts and pigments increased during the period only at the twenty and thirty-five foot depths (Figures 112 through 116). This increased efficiency may have been due to an adaptation to warmer temperatures as the summer progressed. The test temperature for the determination of photosynthetic rate, 20° C., exceeded the highest temperature recorded in the bay. However, as the water in the bay became warmer during the summer, the organisms became accustomed to temperatures more nearly like the test temperature, and therefore performed the photosynthetic reactions more efficiently at that temperature.

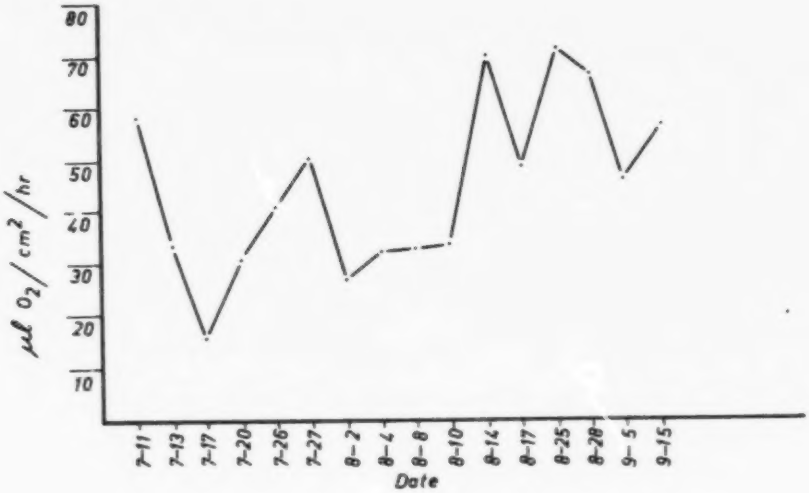

Figure 111. Periphyton Gross Photosynthetic Rates (per unit area) for Samples from 2.5 Feet, Stony Point Bay, Lake Superior, 1967; Run at 20° C., 1500 Foot-Candles.

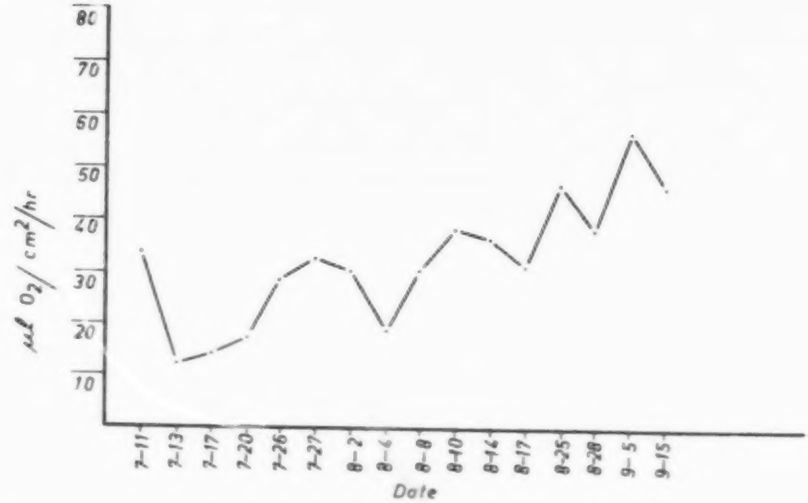

Figure 112. Periphyton Gross Photosynthetic Rates (per unit area) for Samples from Five Feet, Stony Point Bay, Lake Superior, 1967; Run at 20° C., 1500 Foot-Candles.

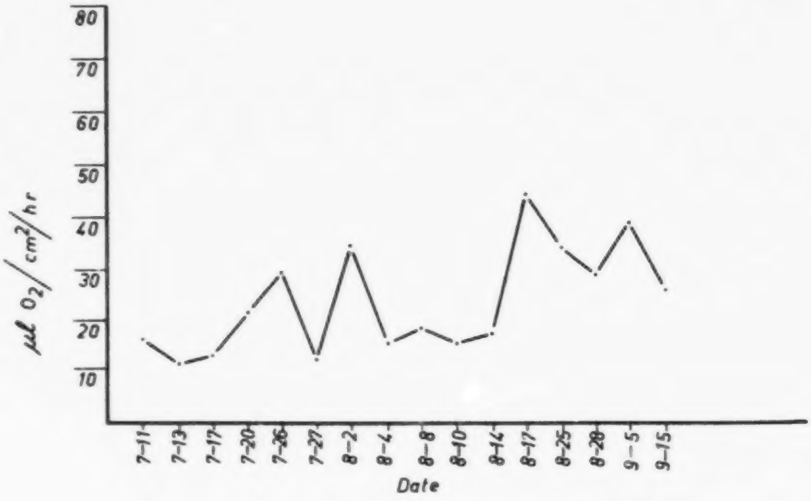

Figure 113. Periphyton Gross Photosynthetic Rates (per unit area) for Samples from Ten Feet, Stony Point Bay, Lake Superior, 1967; Run at 20° C., 1500 Foot-Candles

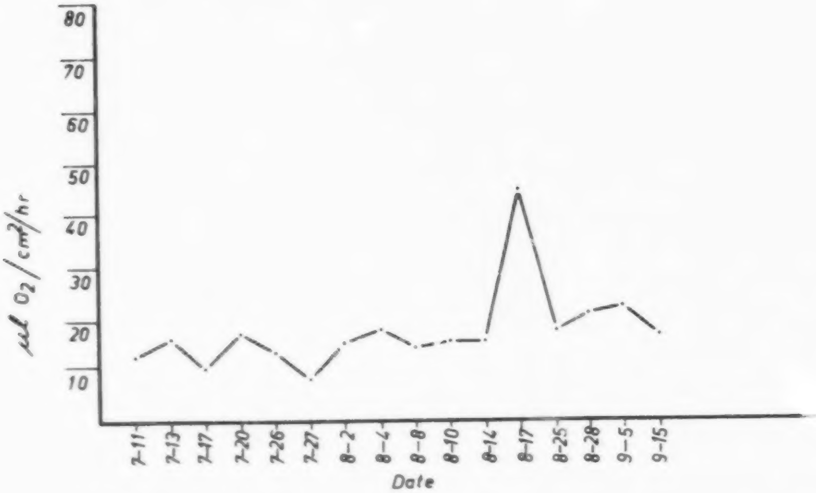

Figure 114. Periphyton Gross Photosynthetic Rates (per unit area) for Samples from Fifteen Feet, Stony Point Bay, Lake Superior, 1967; Run at 20° C., 1500 Foot-Candles

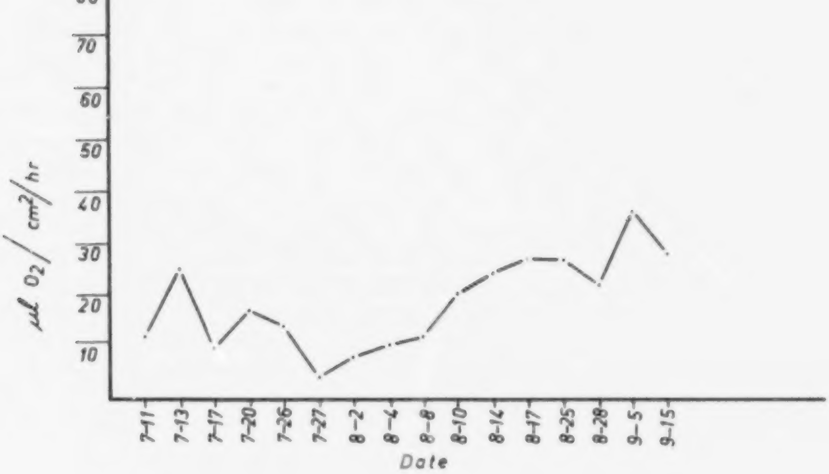

Figure 115. Periphyton Gross Photosynthetic Rates (per unit area) for Samples from Twenty Feet, Stony Point Bay, Lake Superior, 1967; Run at 20° C., 1500 Foot-Candles.

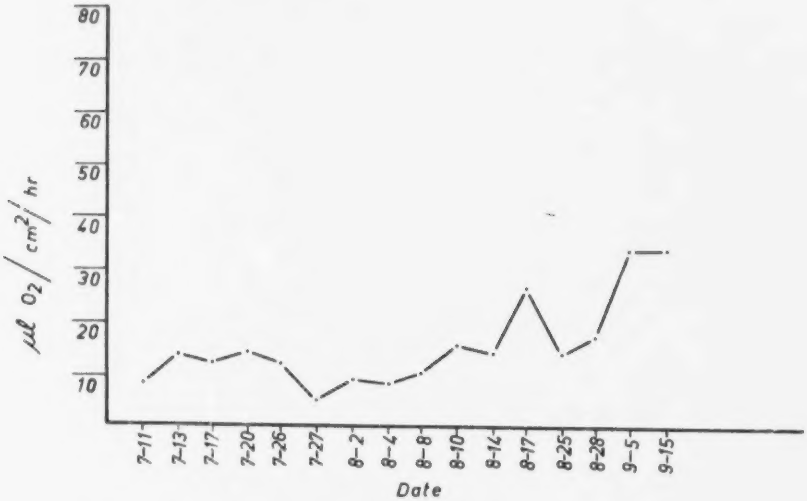

Figure 116. Periphyton Gross Photosynthetic Rates (per unit area) for Samples from Thirty-Five Feet, Stony Point Bay, Lake Superior, 1967; Run at 20° C., 1500 Foot-Candles.

When the production rate in terms of oxygen produced per hour per unit of ash-free dry weight is plotted against sampling depth (Figure 117), it is seen that photosynthetic efficiency depends on the depth from which the sample is taken, as well as on the time of year. The photosynthetic rate is highest (28.8 microliters of oxygen per hour per milligram of ash-free dry weight) for samples from a depth of 2.5 feet, and lowest (13.2 microliters/hour/mg. a.f.d.w.) for samples from thirty-five feet. This trend exactly opposes that exhibited by the amounts of pigment per unit of ash-free dry weight at each depth. When the amount of oxygen produced per unit of chlorophyll is plotted against sampling depth (Figure 118), it may be seen that the values are considerably lower at the twenty and thirty-five foot depths than at the shallower sampling depths. The rates remained quite constant from 2.5 feet to fifteen feet, averaging about 3000 microliters of oxygen per hour per milligram of total chlorophyll. The twenty foot samples evolved 2516 microliter O_2/hour/mg. total chlorophyll, while the thirty-five foot samples produced only 1566 microliters/hour/mg. total chlorophyll. The amount of oxygen evolved per hour per unit of chlorophyll a produced about the same pattern when plotted against depth.

For purposes of comparison with other reported assimilation values, the production rates were also calculated in terms of grams of carbon fixed per hour per gram of total chlorophyll. The value at 2.5 feet was 1.58; at five feet, 1.59; at ten feet, 1.70; at fifteen feet, 1.65; at twenty feet, 1.55; and at thirty-five feet, 0.84. These assimilation numbers are considerably lower than the ones calculated for Stony Point Bay periphyton in 1966. The differences are probably due to the change in methodology employed in the determination of photosynthetic rate. The 1967 mean values represent many more analyses than were run in 1966, and are therefore considered to be more accurate.

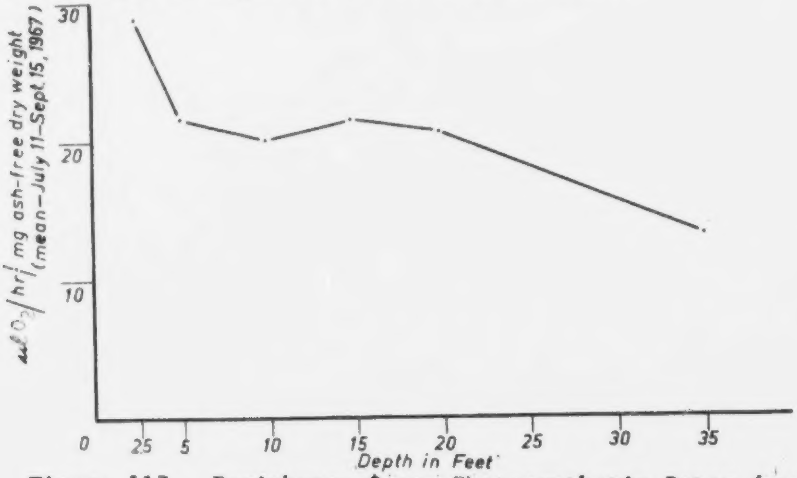

Figure 117. Periphyton Gross Photosynthetic Rates (per unit ash-free dry weight), Stony Point Bay, Lake Superior, 1967.

The apparent decreased efficiency in photosynthesis with increasing depth may be due to adaptation to both temperature and light intensity. It has been shown that temperature decreased with depth; therefore, the organisms grown in the shallow, warmer water would be more apt to function at a more rapid rate at the test temperature (20° C.) than those grown in deep, colder water. Average light intensity has also been shown to decrease as depth increases in the bay. The average intensities at fifteen, twenty and thirty-five feet were lower than in the standard test procedure; the samples from these depths, then, would not be as accustomed to the test intensity as those taken from the shallow depths. In order to further determine the magnitude of variability in the relationship between pigment concentrations and photosynthetic rate, a correlation coefficient was calculated for these two parameters of productivity. The correlation coefficient for the combined data for all depths was 0.573 ($P=0.001$), indicating a rather weak positive correlation.

Correlation coefficients were also calculated for total counts and photosynthetic rate for each sampling depth, to test the seasonal variation in this relationship. Regression lines were also constructed as a means for estimating production rates from numbers of organisms. The regression lines, correlation coefficients (r), and probability values (P) are shown in Figures 119 through 124). The correlations were positive at all depths, but were rather poor except for the thirty-five foot samples. the data for the fifteen foot samples produced the lowest coefficient ($r=0.249$, $P=0.10$); the two measurements correlated best at thirty-five feet ($r=0.844$, $P=0.001$). Generally speaking, one could not expect very accurate predictions of production rates based on enumeration of organisms, even when the sampling depth is known. If the depth were not known, such a prediction would not be at all advisable. The relationship between pigments and counts, and between photosynthesis and counts are apparently variable with respect to time. There are obvious differences in the relationships in terms of the depth at which the organisms grew. These statements should not imply that the differences occur randomly; work performed in 1968 has shown that these differences may be ascribed to environmental factors. As will be seen in a following section, measurements made under standard laboratory conditions may be adjusted to account for existing environmental conditions at the time of sampling.

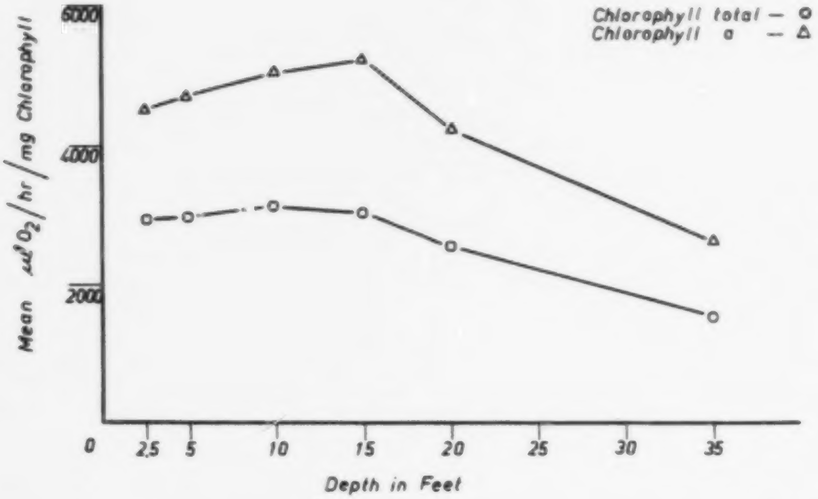

Figure 118. Periphyton Gross Photosynthetic Rates (per unit chlorophyll), Stony Point Bay, Lake Superior, 1967.

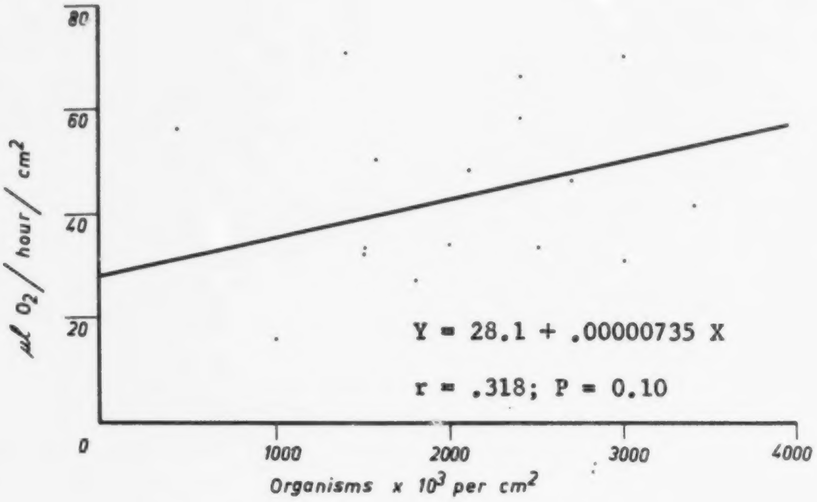

Figure 119. Regression Line, Photosynthetic Rate Versus Counts, Naturally Occurring Periphyton at 2.5 Feet, Stony Point Bay, Lake Superior, 1967

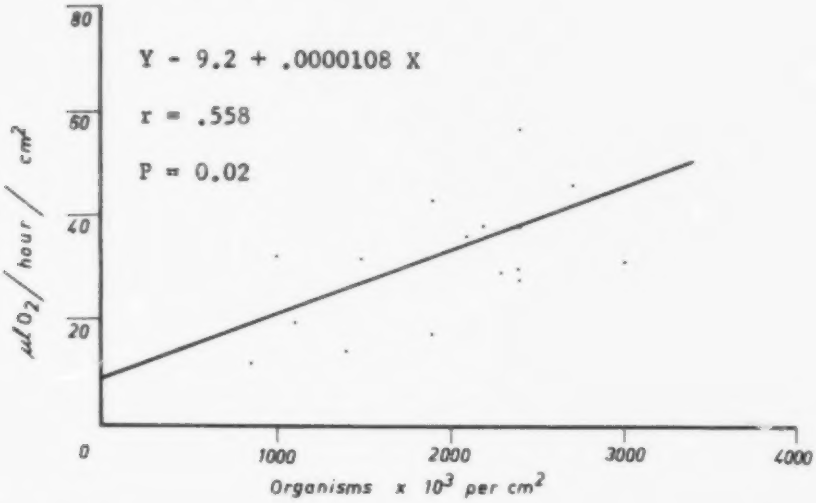

Figure 120. Regression Line, Photosynthetic Rate Versus Counts, Naturally Occurring Periphyton at Five Feet, Stony Point Bay, Lake Superior, 1967.

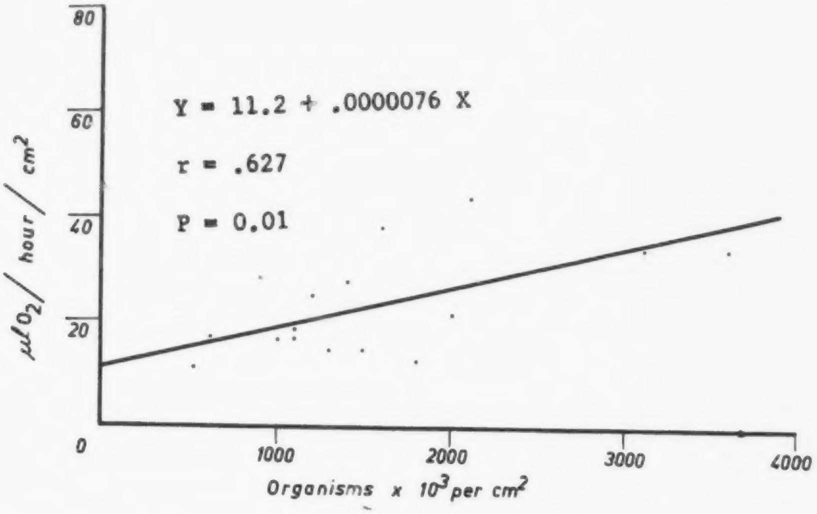

Figure 121. Regression Line, Photosynthetic Rate Versus Counts, Naturally Occurring Periphyton at Ten Feet, Stony Point Bay, Lake Superior, 1967.

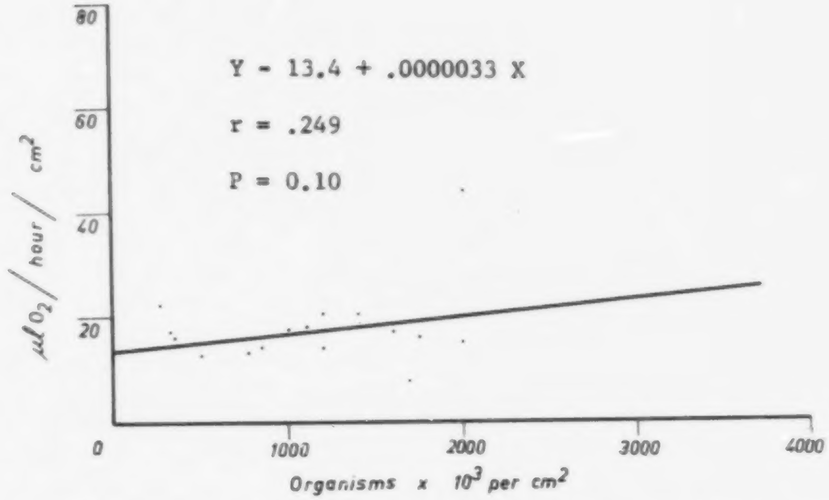

Figure 122. Regression Line, Photosynthetic Rate Versus Counts, Naturally Occurring Periphyton at Fifteen Feet, Stony Point Bay, Lake Superior. 1967.

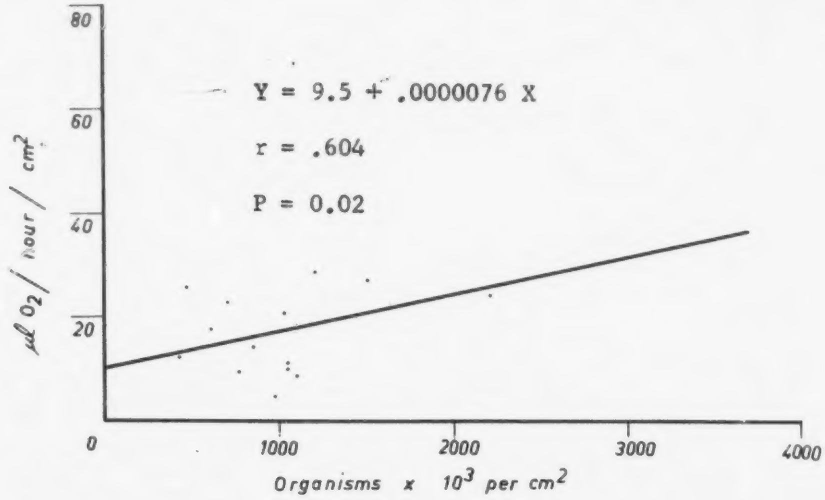

Figure 123. Regression Line, Photosynthetic Rate Versus Counts, Naturally Occurring Periphyton at Twenty Feet, Stony Point Bay, Lake Superior, 1967.

The 1967 photosynthesis data are presented in several ways in Table XXVIII. The average net photosynthetic rate for periphyton samples from all depths was 17.3 microliters of oxygen evolved per hour per square centimeter of rock surface. The ratio of gross photosynthesis to respiration ranged from 2.96 for samples from a depth of fifteen feet to 3.46 for samples from five feet, and averaged 3.17. The photosynthetic rates were converted to net daily production values, as carbon fixed per unit area and as glucose produced per unit area. Net production in terms of carbon fixed varied from 0.57 grams per square meter per day at thirty-five feet to 1.79 grams per square meter per day at 2.5 feet; the average value was 1.01. The mean production rate (as glucose) for all depths was 3.35 grams per square meter per day. For the purpose of calculating mean production rates for the entire bay, it was decided that the data for each of the sampling depths would apply to a strip of the bay as wide as half the distance to the next shallower sampling point plus half the distance to the next deeper sampling point. Since the sampling area was pie-shaped, and since the sampling points were progressively further apart toward the deeper water (see Figure 2), the area corresponding to each sampling depth was virtually the same size; therefore, each production value was given equal weight in the determination of the mean. All of the net photosynthesis data was calculated on the basis of a fifteen-hour day, and takes into account daytime and nighttime respiration.

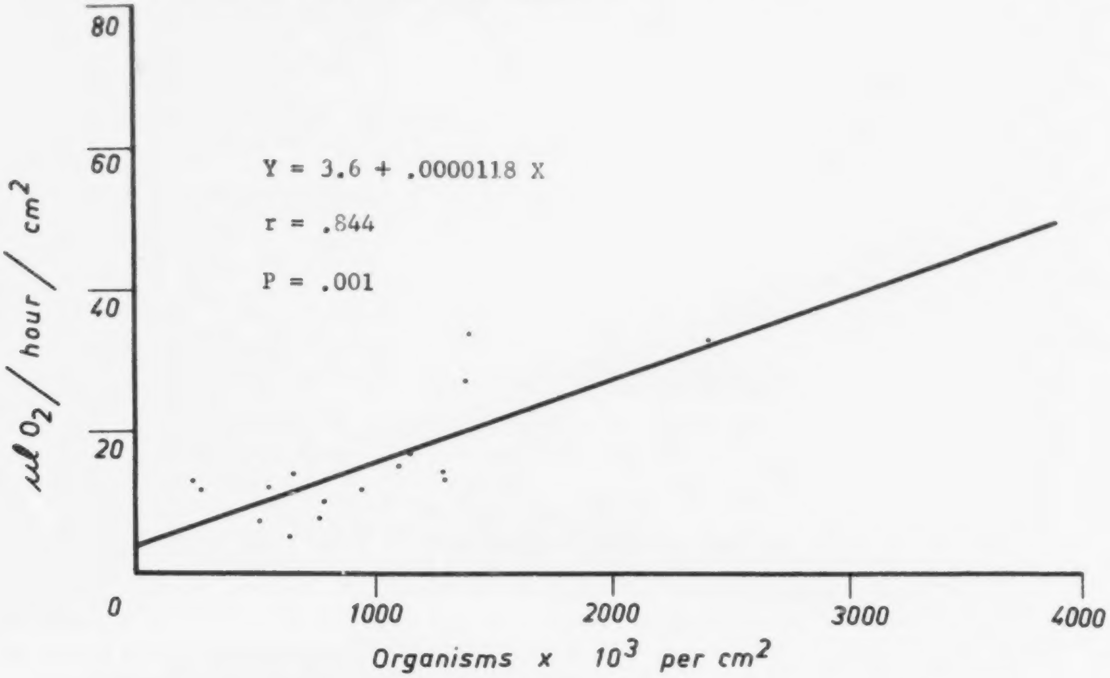

Figure 124. Regression Line, Photosynthetic Rate Versus Counts, Naturally Occurring Periphyton at Thirty-Five Feet, Stony Point Bay, Lake Superior, 1967.

TABLE XXVIII

PHOTOSYNTHESIS DATA FOR PERIPHYTON SAMPLED AT DIFFERENT DEPTHS, STONY POINT BAY, 1967 RUN AT 20°C, 1500 FOOT-CANDLES

	Sampling depth in feet						
	2.5	5	10	15	20	35	Mean
Gross photosynthesis ul $O_2/cm^2/hr$	+44.6	+31.8	+23.0	+17.2	+19.2	+15.3	+25.2
Respiration ul $O_2/cm^2/hr$	-13.9	-9.2	-7.6	-5.8	-5.7	-5.1	-7.9
Net photosynthesis ul $O_2/cm^2/hr$	+30.7	+22.6	+15.4	+11.4	+13.5	+10.2	+17.3
P/R	3.21	3.46	3.03	2.96	3.36	3.00	3.17
Net production							
Grams carbon fixed per M^2 per day	1.79	1.36	0.87	0.63	0.81	0.57	1.01
Grams (as Glucose) per M^2 per day	5.96	4.53	2.90	2.10	2.70	1.90	3.35

The production rates calculated for Stony Point Bay in 1967 may be compared with those reported for other periphyton communities and certain phytoplankton communities. In making such comparisons it is realized that the methodology varies in each investigation and that differences or similarities may often be attributed to methodology. The average rate of carbon fixation by Stony Point Bay periphyton, 1.01 grams/M^2/day, compares rather well with the value reported for the periphyton of the Logan River in Utah (0.6 grams/M^2/day) by McConnell and Sigler (1959). Kobayasi (1961) found a production rate of 0.33 grams of carbon fixed/M^2/day in the natural epilithic periphyton of the Arakawa River in Japan. In both of these investigations, the light and dark bottle oxygen technique was used, possibly producing lower results than would be obtained with a manometric method. In addition, incubation of samples by Kobayasi and by McConnell and Sigler was accomplished by submerging the bottles in water at approximately 11° C., considerably lower than the test temperature (20° C.) used in the Stony Point Bay study. On this basis, one might logically invoke Van't Hoff's law, namely, that the reaction rate doubles for each 10° C. increase in temperature, and raise the Logan River value to 1.2 and the Arakawa River value to 0.66. The nutrient concentrations in the two rivers were quite low, as are those found in Lake Superior. Wetzel (1963) has reported a mean production value of 0.73 grams of carbon fixed/M^2/day for the periphyton of Borax Lake, in California. The actual production rates in the four periphyton communities compared above are probably very similar.

Carbon fixation rates for communities other than periphyton are quite variable and include a wide range of reported values. For instance, Odum (1957) has shown the production rates in eleven Florida springs, including the plankton and the periphyton, to range from 0.17 to 18.1 grams of carbon fixed/M^2/day. A value of 0.49 grams of carbon fixed/M^2/day for the phytoplankton of Weber Lake, in Wisconsin, has been reported by Manning and Juday (1941). Hogetsu and Ichimura (1954) determined the mean production rate for the phytoplankton of Japan's Lake Suwa to be 0.44 grams of carbon fixed/M^2/day. Data provided by Olson and Putnam (1961) show that the phytoplankton of Lake Superior at Larsmont, not far from Stony Point Bay, fix an average of 0.17 grams of carbon per square meter per day during the summer months. Based on this result, it is concluded that the periphyton of Stony Point Bay can produce five to six times as much organic matter as the phytoplankton in the area within one-half mile of shore.

In 1967, the periphyton of Stony Point Bay contained 0.097 grams of chlorophyll per square meter of rock surface. This value is lower than the mean yearly chlorophyll concentration in the periphyton of the Logan River (0.30 grams/M^2) as measured by McConnell and Sigler (1959), and somewhat higher than the 0.040 grams/M^2 reported by Kobayasi (1961) for the Arakawa River periphyton. The periphyton growing in the Arakawa River at the time of Kobayasi's investigation was made up primarily of diatoms. Wetzel (1963) found the mean concentration of chlorophyll in the periphyton of Borax Lake to be 0.32 grams/M^2. Values ranging from 0.43 to 2.01 grams of chlorophyll/M^2 in laboratory streams have been recorded as the communtities changed from those dominated by diatoms to those dominated by Phormidium (McIntire and Phinney, 1965).

According to Odum (1959), Gessner has stated that the chlorophyll of diverse communities develops in very similar amounts on a square meter basis, thus providing an example of "community homeostasis." In light of this contention, it is interesting to compare the chlorophyll concentration of Stony Point Bay periphyton (0.097 grams per M^2) with the concentrations in phytoplankton communities. The concentration of chlorophyll in Lake Superior phytoplankton at the Larsmont station during the summer of 1961 averaged 0.017 grams/M^2 (calculated from data presented by Putnam and Olson, 1961). According to Hogetsu and Ichmura (1954), the phytoplankton of Lake Suwa also supported less chlorophyll (0.066 grams per M^2) than Stony Point Bay periphyton. However, a much higher value, 0.27 grams/M^2, has been reported for the Gerlache Straits of Antarctica by Burkholder and Sieburth (1961).

Very little information is available regarding assimilation values for periphyton communities. The mean assimilation value for Stony Point Bay periphyton was 1.4 grams of carbon fixed per hour per gram of chlorophyll, according to the 1967 data. This figure compares well with those reported for the epilithic periphyton of the Arakawa River by Kobayasi (1961). When measured at a light intensity of 30 000 lux (2778 foot-candles), the organisms fixed 0.75 grams of carbon/hour/gram of chlorophyll at 12° C. and 1.9 grams of carbon/hour/gram of chlorophyll at 26° C. McConnell and Sigler (1959) report an assimilation value of 0.75 grams of carbon fixed/hour/gram of chlorophyll in the periphyton of the Logan River. These figures agree very well with the assimilation value calculated for Stony Point Bay periphyton under the test conditions. Since certain accessory pigments have been shown to be active in photosynthesis, an assimilation value based on total pigments should be calculated for all communities studied, so that the photosynthetic efficiencies of diverse communities can be more accurately compared in the future. For the periphyton of Stony Point Bay this value would be 1.12 grams of carbon fixed/hour/gram of total pigment.

It is difficult to compare the weights of Stony Point Bay periphyton with weights reported for other periphyton communities because most other investigations have involved the use of suspended glass slides for the accumulation of organisms. Periphytic communities developing on these slides do not contain the significant amounts of sand and clay that are found in natural communities. The periphyton developing on glass plates in several freshwater lakes in Washington produce an average dry weight of only 0.15 grams per square meter, compared to 156 grams per square meter for Stony Point Bay periphyton. Corresponding organic weights were 0.015 and 12 grams per square meter. The organic weight of the material in the Washington lakes was 34 per cent of the dry weight, while the organic weight of the Stony Point Bay periphyton was only 7.7 per cent of the dry weight; this discrepancy emphasizes the fact that natural communities contain large amounts of sand. Newcombe (1950) reports that the periphyton developing on glass slides in Sodon Lake, Michigan, produced dry weights ranging from 0.5 to 2.0 grams/M^2 and ash-free dry weights varying between 0.16 and 0.95 grams/M^2 (32 to 49 per cent). The average dry weight of the natural epilithic community in the Logan River was shown to be 25 grams/M^2 (McConnell and Sigler, 1959), while the periphyton community of Sedlice Reservoir, in Czechoslovakia, weighed 15.9 grams/M^2 (Sladecek and Sladeckova, 1963). According to Atkins and Parke (1951), the chlorophyll of many marine algae makes up from 2.3 to 2.9 per cent of the organic weight. The chlorophyll of Stony Point Bay periphyton accounts for only 0.8 per cent of the organic weight.

Considering the data as a whole, the periphyton of Stony Point Bay as measured by several parameters seems to be indicative of an oligotrophic situation. The pigment ratios indicate a community dominated by diatoms. The measures of biomass show that the growths are of average magnitude when compared with the communities of other bodies of relatively clean water. The production rate in the bay, based on photosynthetic activity, is also similar to the rates exhibited by the periphyton of mountain streams, springs and other cold lakes.

Periphyton Regrowth, Stony Point Bay

From July 31 to November 9, 1967, a study to determine the rate of establishment of periphyton organisms on denuded, autoclaved rocks was conducted in Stony Point Bay. In the course of the study, eighty-four rocks were recovered from the three stations where they had been placed on July 31. These stations were at depths of ten, twenty and thirty-five feet. Selected "incubation times" ranged from eight hours to 101 days. On the final sampling day, November 9, samples were collected only at the thirty-five foot depth, because the marker buoys for the other two stations had been dislodged by a storm.

The amounts of chlorophylls *a*, *b*, and *c* per unit area of rock surface at each sampling time are presented in Figures 125 through 127. In general, the chlorophyll concentrations increased continually during the study period, rising to a maximum at all three depths on September 15, the last day on which all depths were sampled. On any given day, the amount of chlorophyll per unit area was found to be about equal at the three depths. At the ten foot depth, chlorophyll *a* increased from 0.004 milligrams per 100 square centimeters to 0.165 milligrams per 100 square centimeters during the forty-six day period. The chlorophyll *a* concentration at twenty feet began at 0.004 mg/100 cm^2 and rose to 0.213 mg/100 cm^2, while at thirty-five feet, the concentration increased from 0.003 mg/100 cm^2 to 0.185 mg/100 cm^2. The concentration of chlorophyll *a* at the thirty-five foot depth had dropped to 0.108 mg/100 cm^2 by November 9 (101 days). The only other depression occurred on August 28, and was apparent in both the ten and thirty-five foot samples.

Chlorophyll *c*, chlorophyll *b*, and non-astacin carotenoids were present in about the same relative amounts as in the naturally occurring periphyton of Stony Point Bay, indicating that the same types of organisms were present. All of the pigment groups increased with time except the astacin carotenoids, which varied between 0.002 and 0.015 MSPU/100 cm^2 at all three depths and were as low on September 15 as they were on August 4 (0.004 MSPU/100 cm^2). The varying astacin carotenoid concentrations are probably indicative of the presence of inconsistent numbers of Cladocerans in association with the attached algae. The ratio of chlorophyll *c* to chlorophyll *a* varied widely during the sampling period, occasionally exceeding unity when the total concentrations were very low. On the other hand, the increase in the concentration of non-astacin carotenoids during the summer closely paralleled that of the chlorophyll *a* concentration; the ratio of non-astacin carotenoids to chlorophyll *a* did not vary significantly from 0.360 at ten feet, 0.312 at twenty feet, and 0.302 at thirty-five feet. Chlorophyll *b* concentrations remained quite low throughout the period, reaching a maximum of

0.035 mg. per 100 cm^2 at the twenty foot depth on August 28. Since the chlorophyll b concentration also peaked on the same date at the other sampling depths, it appears that the relative number of green algae in the regrowth material reached a maximum on that date.

When the total chlorophyll concentrations obtained on the last regular day of sampling (September 15) are divided by their "incubation" time (forty-six days), daily production rates are produced. The daily rates for accumulation of chlorophyll at ten, twenty and thirty-five feet are 0.00046, 0.00069, and 0.00056 grams per square meter per day. No other investigations have been encountered in which the measurement of chlorophyll has been employed to determine the rate of periphyton accumulation on a natural substrate in the lentic situation. However, while observing the growth of periphyton on concrete cylinders in a river, Waters (1962) found that three to eight weeks were required for the chlorophyll concentration to reach a maximum level. Past that point, seasonal variations were shown.

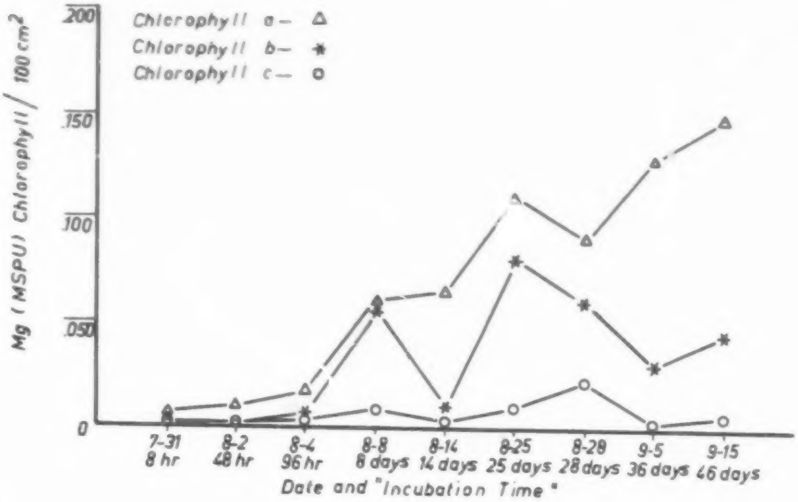

Figure 125. Regrowth Periphyton Chlorophyll Concentrations (per unit area) at Ten Feet, Stony Point Bay, Lake Superior, 1967.

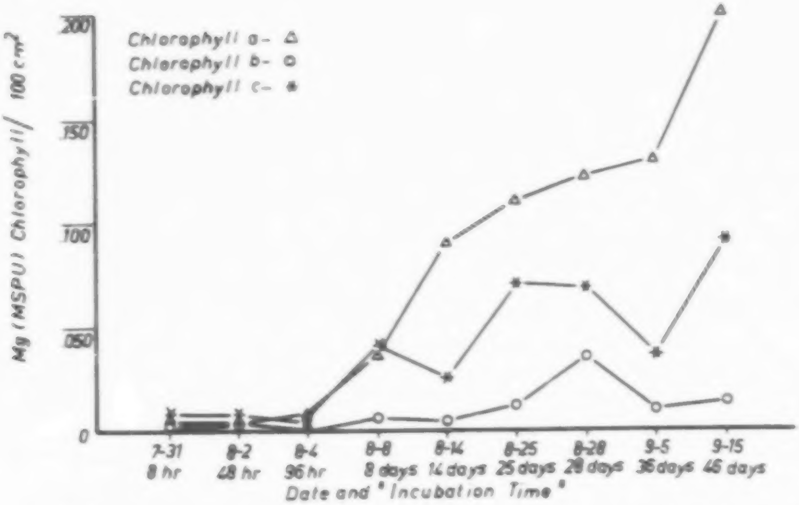

Figure 126. Regrowth Periphton Chlorophyll Concentrations (per unit area) at Twenty Feet, Stony Point Bay, Lake Superior, 1967.

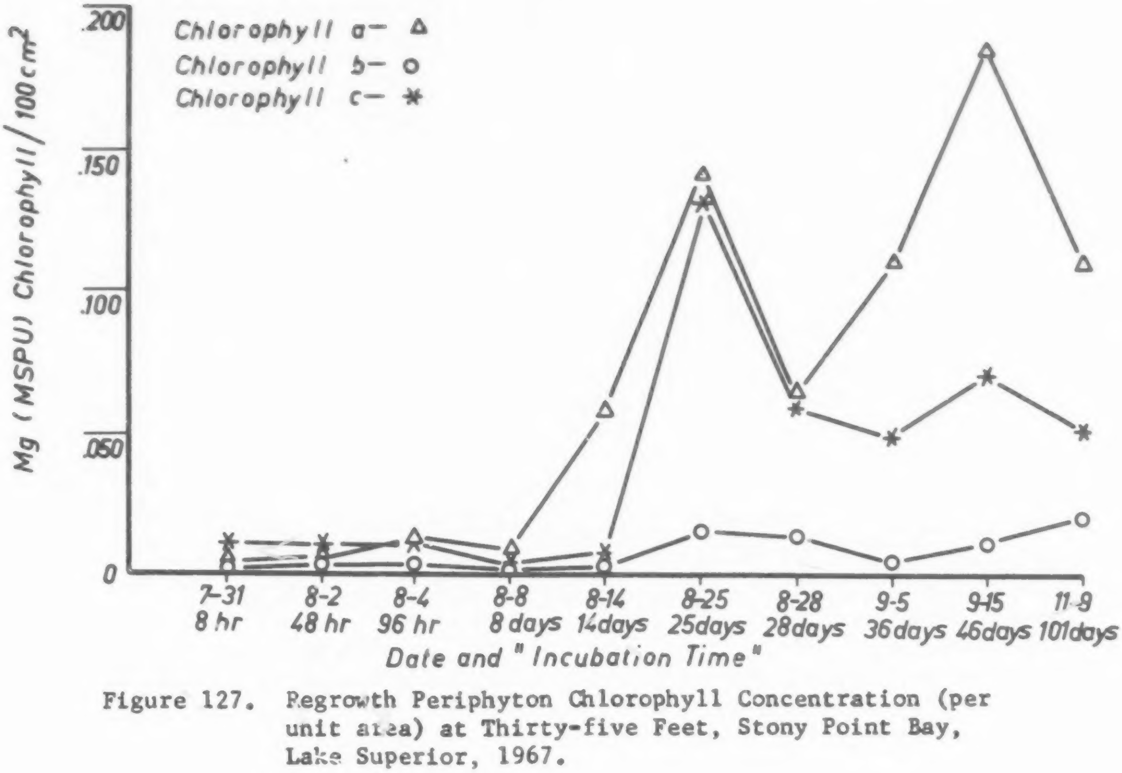

Figure 127. Regrowth Periphyton Chlorophyll Concentration (per unit area) at Thirty-five Feet, Stony Point Bay, Lake Superior, 1967.

The total dry weights and ash-free dry weights of the regrowth periphyton are shown in Table XXIX. The weights generally increased during the regrowth period at all depths. The daily production rate in terms of total dry weight at ten feet was 5.76 grams/M^2/day; at twenty feet, 2.26 grams/M^2/day; and at thirty-five feet, 2.77 grams/M^2/day. Comparable figures for the rate of ash-free dry weight production are 0.09, 0.05, and 0.06 grams/M^2/day. It is believed that the varying types of rocks which made up the substrata did not affect the growth of periphyton in any way. All rocks "incubated" for a given length of time at a certain depth supported approximately equal amounts of biomass per unit surface area.

Several investigators have reported the rate of increase in organic weight as periphyton accumulated on glass slides or plates. For instance, Kevern _et al_. (1966) have shown that the communities colonizing plexiglass plates in their laboratory streams produced an average of 0.6 grams of organic matter per square meter per day. In their study of the Red Cedar River, in Michigan, King and Ball (1966) found that growth on plexiglass plates amounted to about 0.3 grams per square meter per day. Using glass slides as a substrate, Castenholz (1960) reported production rates up to 0.5 grams of organic weight per square meter per day for lakes in the state of Washington. He believed that glass was not too selective as a substrate for growth of periphyton and that submergence for two weeks was sufficient for the determination of production rates. Foerster and Schlicting (1965), on the other hand, working with glass slides, stated that "the artificial surface gave a flase impression of the productivity trends and indicated only some of the significant genera present in the ecosystem." Thus, in spite of the fact that in general, one might expect that artificial media would result in lower production figures, the production rates reported for stream periphyton growing on artificial substrata are often higher than those for Stony Point Bay periphyton. The average increase in organic weight at the three sampling depths in the bay was 0.066 grams per square meter per day. It must be remembered, however, that the regrowth substrata were placed at depths of ten, twenty, and thirty-five feet in Lake Superior; the light intensities and temperatures at these depths were lower than those reported for streams in which production was very high.

The ash-free dry weights of the Stony Point Bay regrowth were lower at twenty and thirty-five feet than at ten feet during the entire sampling period. Since the chlorophyll concentrations were of virtually the same magnitude at all depths, the amount of chlorophyll per unit of ash-free dry weight was higher at the twenty and thirty-five foot depths than at the ten foot depth. This difference occurred on nearly every sampling day. In order to test the significance of the chlorophyll concentration as a measure of biomass accumulation, correlation coefficients were calculated for total chlorophyll and total numbers of organisms at each depth. The two parameters correlated very well, the coefficients ranging from +0.782 ($P = 0.02$) at the thirty-five foot depth to +0.992 ($P=0.001$) at the twenty foot depth. The coefficient for the ten foot samples was +0.950 ($P = 0.001$). Regression lines for the estimation of numbers of organisms from the regrowth chlorophyll concentrations at each depth are shown in Figures 128 through 130. Good correlation at each depth indicates that chlorophyll concentration is a good parameter of the biomass of periphyton as long as sampling is always done at the same depth.

The photosynthetic rates exhibited by the regrowth samples did not increase smoothly on a unit area basis as did the pigment concentrations and weights (see Figure 131). For the first five days of incubation, no oxygen production could be demonstrated by use of the respirometer. However, on August 8, the photosynthetic rate for the ten foot sample was 5.54 microliters of oxygen per hour per square centimeter, for the twenty foot sample, 4.65 microliters/hour/cm^2; and for the thirty-five foot sample, 3.85 microliters/hour/cm^2. Corresponding values for August 14 were 23.1, 19.5, and 21.1 microliters/hour/cm^2. After August 14, the rates decreased rather than following the general pattern of increase exhibited by the parameters of biomass. The rates at ten, twenty, and thirty-five feet on September 15 were 14.8, 12.6, and 17.6 microliters/hour/cm ^{2}. Until August 14, the ten foot samples produced the highest photosynthetic rate; after that date, the thirty-five foot samples showed the greatest photosynthetic activity. The photosynthetic rates, on a unit area basis, did not correlate well at all with total numbers of organisms. In fact, the correlation coefficients were negative at all depths, ranging from =0.213 (P=0.10) for the twenty foot samples to -0.791 (P=0.01) for the ten foot samples.

TABLE XXIX

DRY AND ASH-FREE DRY WEIGHTS OF PERIPHYTON OCCURRING AS REGROWTH, STONY POINT BAY, LAKE SUPERIOR, 1967 MILLIGRAMS PER SQUARE CENTIMETER OF ROCK SURFACE

Dry Weight				Ash-Free Dry Weight			
	Depth in Feet				Depth in Feet		
Date	10	20	35	Date	10	20	35
7-31	0.68	0.28	0.62	7-31	0.06	0.02	0.04
8-2	0.54	0.27	0.30	8-2	0.17	0.01	0.09
8-4	1.65	0.80	0.59	8-4	0.23	0.18	0.17
8-8	1.92	1.83	0.78	8-8	0.45	0.13	0.13
8-14	5.03	6.96	5.36	8-14	0.64	0.57	0.54
8-25	13.18	7.49	12.82	8-25	1.21	0.52	0.77
8-28	16.53	11.71	6.10	8-28	0.49	0.37	0.26
9-5	7.97	9.48	4.22	9-5	1.03	0.40	0.75
9-15	26.49	10.41	12.75	9-15	0.43	0.24	0.29
11-9	-*	-*	7.02	11-9	-*	-*	0.13

* No sample collected

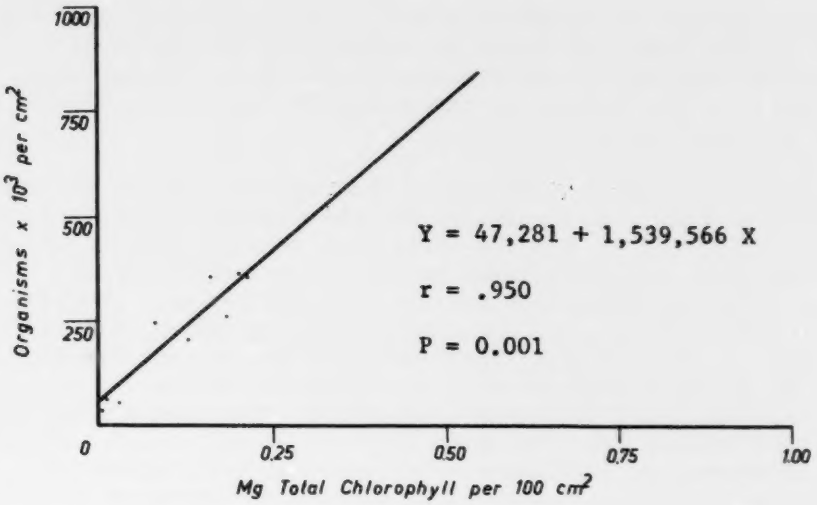

Figure 128. Regression Line, Counts Versus Total Chlorophyll, Regrowth Periphyton at Ten Feet, Stony Point Bay, Lake Superior, 1967.

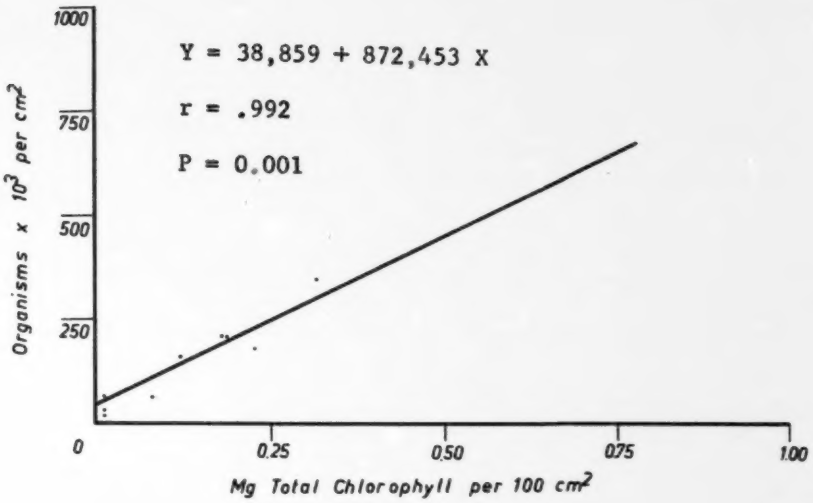

Figure 129. Regression Line, Counts Versus Total Chlorophyll, Regrowth Periphyton at Twenty Feet, Stony Point Bay, Lake Superior, 1967.

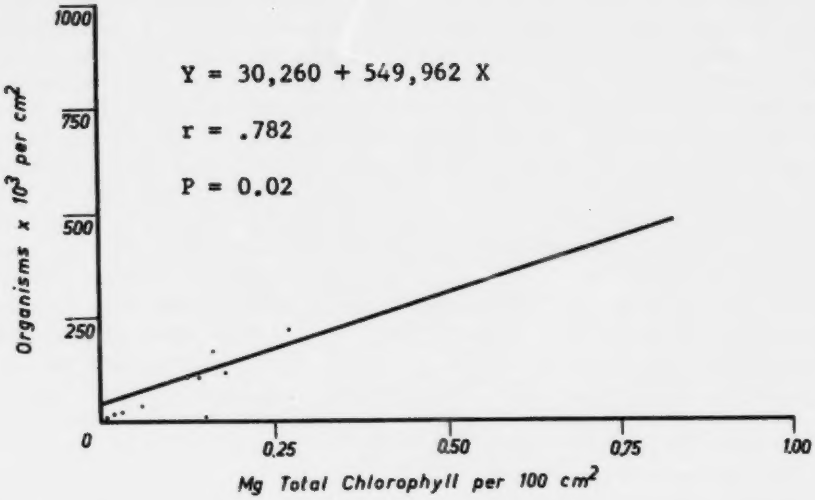

Figure 130. Regression Line, Counts Versus Total Chlorophyll, Regrowth Periphyton at Thirty-Five Feet, Stony Point Bay, Lake Superior, 1967.

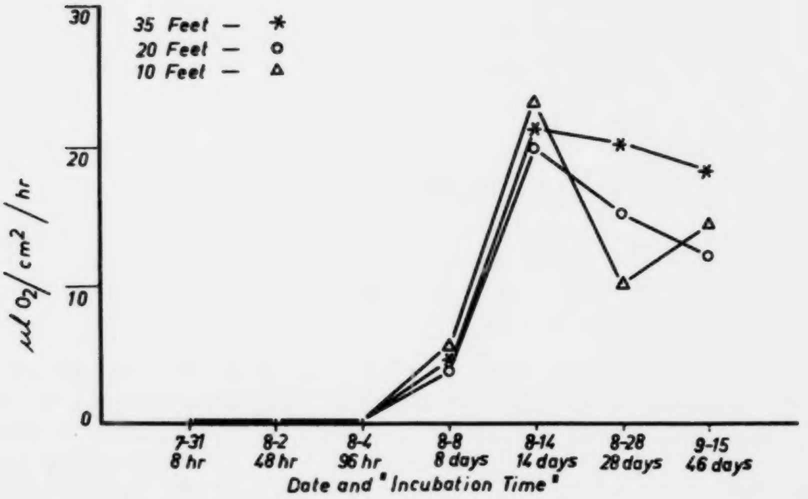

Figure 131. Regrowth Periphyton Photosynthetic Rates (per unit area), Stony Point Bay, Lake Superior, 1967; Run at 20° C., 1500 Foot-Candles.

When the photosynthetic rates were expressed as assimilation values rather than on a unit area basis, the inconsistency in photosynthetic efficiency during the regrowth period became obvious. For example, the assimilation value for the twenty foot sample on August 8 was 3.01 grams of carbon fixed per hour per gram of chlorophyll; however, by August 14 the value had risen to 8.53 grams C/hour/gram of chlorophyll. The assimilation value returned to 3.04 grams C/hour/gram of chlorophyll on August 28, and then fell further to 2.06 grams C/hour/gram of chlorophyll on September 15. All of these values are higher than those calculated for naturally occurring periphyton in Stony Point Bay in 1967, although by September 15, the figures are not significantly different. By comparing the highest total chlorophyll concentrations attained during the regrowth study (September 15) with the average concentration for the naturally occurring periphyton of Stony Point Bay, it is seen that the regrowth never approached the natural level. At ten feet, the amount of chlorophyll in the regrowth sample was only twenty-nine per cent of that present in the naturally occurring growth; corresponding figures for the twenty and thirty-five foot depths are forty-two and twenty-seven per cent. However, the photosynthetic rate of the regrowth samples, on a unit area basis, reached ninety-nine per cent of the rate exhibited by the natural population at the ten foot level. At the twenty foot depth, the figure was 101 per cent, and at thirty-five feet, seventy-two per cent. It is not surprising that the regrowth population reacted in a different manner to the test conditions than did the natural population. Waters (1961) stated that developing populations cannot be expected to reflect the same relationship to external factors as those which have long since reached a maximum level of biomass. That contention is strongly supported by the apparent discrepancy between the photosynthetic rates of natural and regrowth periphyton communities under the standard test conditions.

Naturally Occurring Periphyton

Stations other than Stony Point Bay.

In an accessory study, periphyton samples were taken at eleven points along the north shore other than Stony Point Bay. The stations used are indicated in Table XXX and Figure 3. Collections were made from the standard depths and on two separate occasions.

The organisms growing in these areas were studied primarily to determine whether there are significant local differences in the amount, type, and activity of the periphyton of Lake Superior's north shore. In other words, the study was conducted to test the hypothesis that the periphyton community of the prime sampling area, Stony Point Bay, was representative of a large segment of the western arm of the lake. The only data which are discussed in detail are those which appear to be unusual.

The results of the north shore investigayion are summarized in Table XXXI. For the purpose of comparing the various periphyton communities, the average amount of total pigment from all depths on the two sampling days was calculated for each station. The individual concentrations of chlorophylls a, b, and c at each sampling depth are presented in Figures 132 through 152.

The mean dry and ash-free dry weights for each station are included in the summary table XXXI. The average photosynthetic rate, on a unit area basis, at the 2.5 and twenty foot depths may also be seen in the summary table.

The total pigment concentrations of north shore periphyton ranged from 0.338 milligrams per 100 square centimeters of rock surface at Sugar Loaf Cove to 3.590 milligrams per 100 square centimeters at Lester River. The mean for all of the stations was 1.363 milligrams of pigment /100 cm^2. This value compares well with the average concentration of pigment in Stony Point Bay periphyton during the same summer (1.181 $mg/100\ cm^2$). The area supporting the least extensive biomass, Sugar Loaf Cove, is the site of an extensive logging operation. The cove is often used as a storage area for floating logs; during such period, the light intensity at the bottom of the cove is severely diminished. Low water temperature also limited the periphyton growth at Sugar Loaf Cove. Temperatures of 5.5° C. at a depth of twenty feet and 7.0° C. at the surface were recorded on August 31. The ratio of chlorophyll b/chlorophyll c in the periphyton in the cove, 0.143, indicated that diatoms dominated that community to an even greater extent than in Stony Point Bay. Only two other sampling areas, Tofte and No-Name Bay, supported significantly less periphyton biomass than Stony Point Bay, as indicated by pigment concentrations.

TABLE XXX

PERIPHYTON SAMPLING LOCATIONS ALONG THE NORTH SHORE OF LAKE SUPERIOR

Location	Distance from Lester River in miles
1. Lester River	0
2. Knife River	13.8
3. Burlington Bay	22.1
4. Split Rock River Bay	39.4
5. Beaver Bay	48.0
6. No-Name Bay (near Little Marais)	53.9
7. Sugar Loaf Cove	69.9
8. Tofte	78.8
9. Lutsen	86.3
10. Good Harbor Bay	100.9
11. Grand Marais	106.9

TABLE XXXI

SUMMARY OF RESULTS, NORTH SHORE STATIONS, LAKE SUPERIOR, 1967

Study Area	Mean Total Pigment Conc.*	Mean Weights**		Chl. b/c	Production Rate***	
		Dry	Ash-free		2.5 feet	20 feet
Lester River	3.590	19.5	1.46	0.568	18.7	44.1****
Knife River	1.033	9.5	1.16	0.324	15.4	23.1
Burlington Bay	1.052	16.6	1.50	0.359	51.8	35.8****
Split Rock River Bay	1.256	12.5	1.35	0.347	63.9	20.2
Beaver Bay	1.264	31.5	2.31	0.402	15.2	19.0
No-Name Bay	0.767	5.6	0.84	0.413	20.3	22.2
Sugar Loaf Cove	0.338	2.7	0.61	0.143	18.8	15.2
Tofte	0.665	5.5	0.97	0.411	19.4	17.2
Lutsen	1.194	9.5	0.89	0.331	69.7	16.8
Good Harbor Bay	1.131	10.5	1.51	0.405	28.7	21.9
Grand Marais	2.700	16.0	1.60	0.588	33.3	54.5
Mean	1.363	12.7	1.29	0.390	32.3	26.4

* Mg + MSPU/100 cm^2

** Mg/cm^2

*** Microliters $O_2/hour/cm^2$

**** 15 feet

The pigment concentrations, on a unit area basis, were considerably higher at both Lester River and Grand Marais than at Stony Point Bay. In addition, a relatively high ratio of chlorophyll *b*/chlorophyll *c* at these stations indicated the presence of a substantial percentage of green algae in the periphyton. The ratios of chlorophyll *b*/*c* at Lester River (0.568) and Grand Marais (0.588) were much higher than the ratio at Stony Point Bay (0.366). Microscopic examination of samples revealed that the Lester River station was the only area which supported the growth of *Cladophora*, and that a rather heavy crop of *Ulothrix* was present at Grand Marais. Since only the Lester River and Grand Marais stations are near relatively large population centers, it is possible that local sewage effluents were partially responsible for the support of more extensive and more varied periphyton communities at these stations than in the other areas. The relatively high water temperature at the Lester River station probably contributed in large measure to the moderately heavey growth of *Cladophora*. According to Neil and Owen (1964), the growth of *Cladophora* has reached nuisance proportions in Lake Erie and Lake Ontario. The present study has shown that green algae are of minor importance in the periphyton communities of the western arm of Lake Superior. Even at the Lester River and Grand Marais stations, diatoms are the dominant algal type among the attached algae.

The dry and ash-free dry weights of the north shore periphyton were quite variable. The number of samples taken was not sufficient to allow the correlation of the weights with other parameters of biomass. The samples from Beaver Bay contained small (ten to twenty microns) black magnetic particles which adhered to the periphyton mass on the rocks. Although the total pigment concentration, on a unit area basis, in the periphyton of Beaver Bay was less than the average value for all the north shore stations, the dry weight was the highest encountered anywhere.

The gross production rates at the north shore stations, as measured by respirometry under standard conditions, were similar to those exhibited by the periphyton of Stony Point Bay. The average photosynthetic rate for organisms from a depth of 2.5 feet at all stations, 32.3 microliters of oxygen/hour/cm^2, was lower than that recorded at Stony Point Bay (44.6 microliters O_2/hour/cm^2); however, the samples from a depth of twenty feet produced 26.4 microliters O_2/hour/cm^2, compared with 19.2 microliters O_2/hour/cm^2 for the twenty foot samples from Stony Point Bay

The types and numbers of organisms comprising the periphyton are not drastically different at any point along the 107 mile segment of the north shore of Lake Superior. Stony Point Bay would seem to qualify as a representative area for future study of the effects of changes in water quality on the condition of this community in the western arm of Lake Superior.

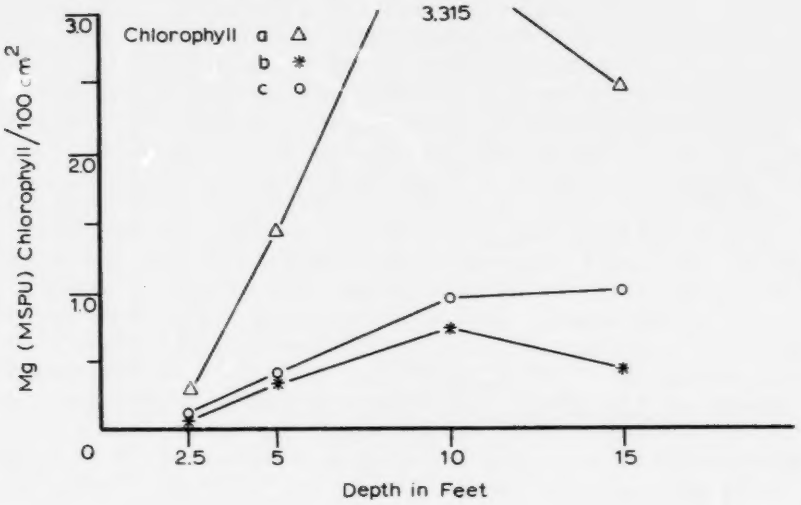

Figure 132. Periphyton Chlorophyll Concentrations (per unit area) at Standard Depths, Lester River Station, Lake Superior, August 16, 1967.

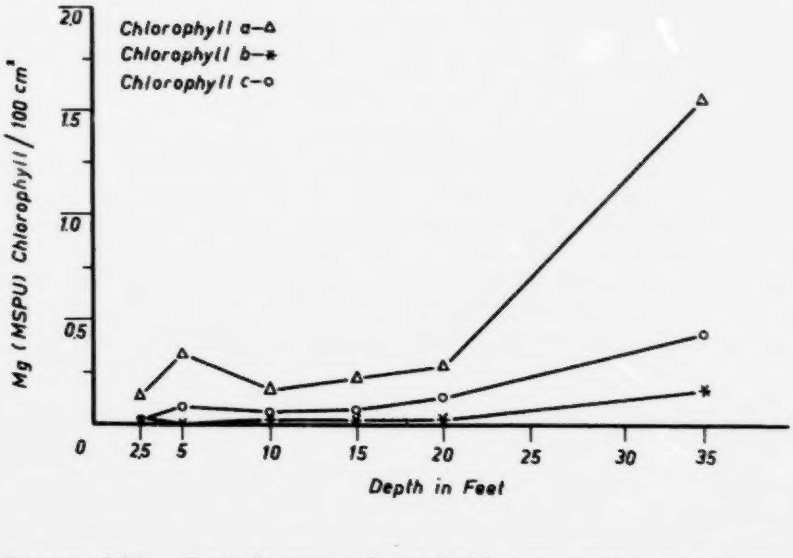

Figure 133. Periphyton Chlorophyll Concentrations (per unit area) at Standard Depths, Knife River Station, Lake Superior, September 5, 1967.

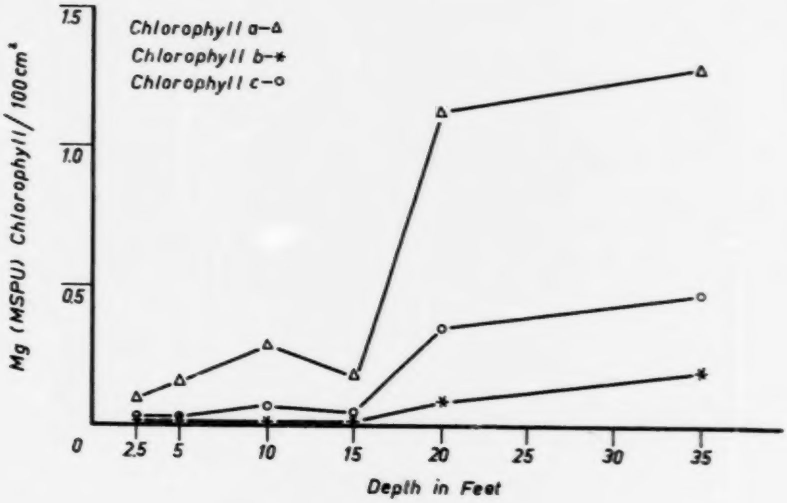

Figure 134. Periphyton Chlorophyll Concentrations (per unit area) at Standard Depths, Knife River Station, Lake Superior, September 15, 1967.

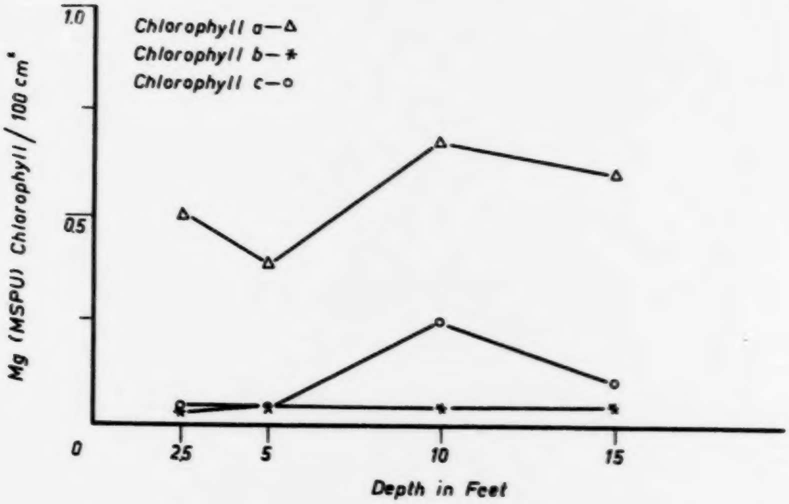

Figure 135. Periphyton Chlorophyll Concentrations (per unit area) at Standard Depths, Burlington Bay, Lake Superior, August 22, 1967.

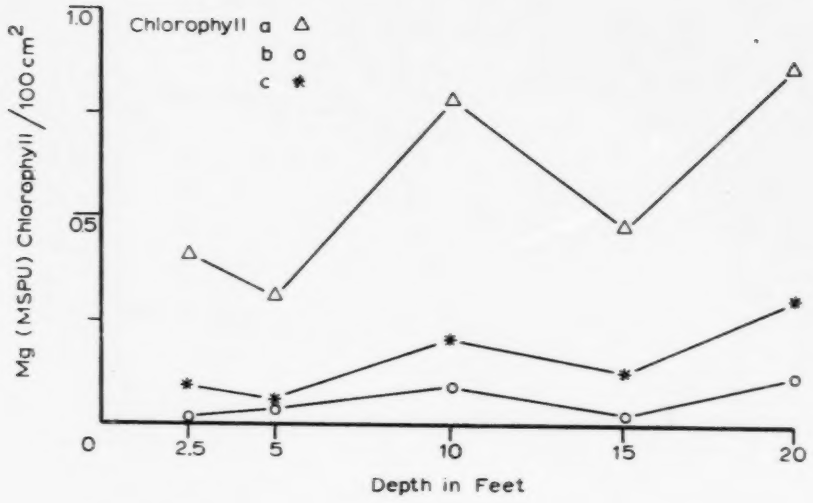

Figure 136. Periphyton Chlorophyll Concentrations (per unit area) at Standard Depths, Burlington Bay, Lake Superior, September 1, 1967.

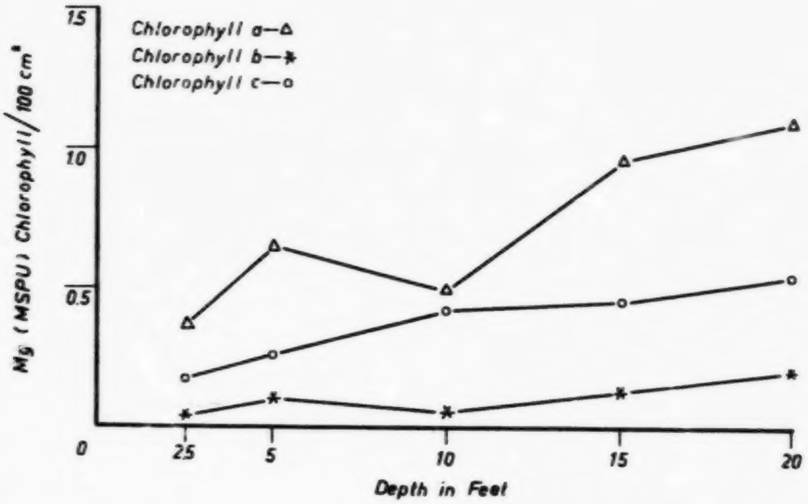

Figure 137. Periphyton Chlorophyll Concentrations (per unit area) at Standard Depths, Split Rock River Bay, Lake Superior, August 29, 1967.

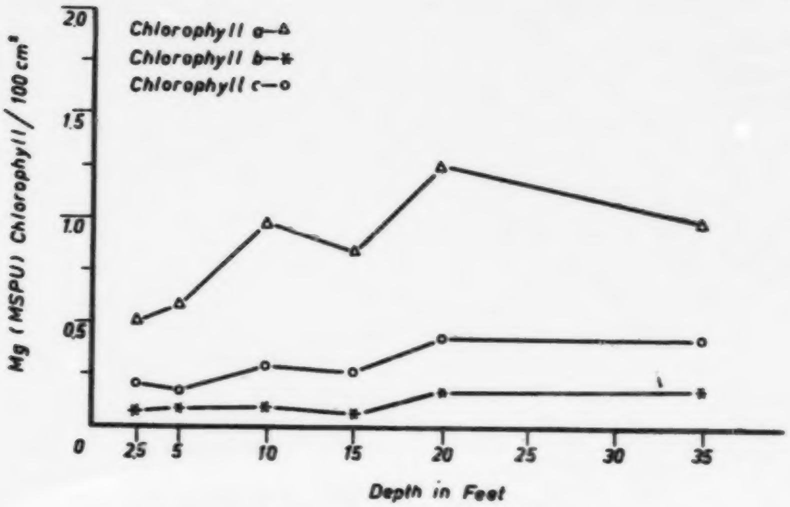

Figure 138. Periphyton Chlorophyll Concentrations (per unit area) at Standard Depths, Split Rock River Bay, Lake Superior, September 7, 1967.

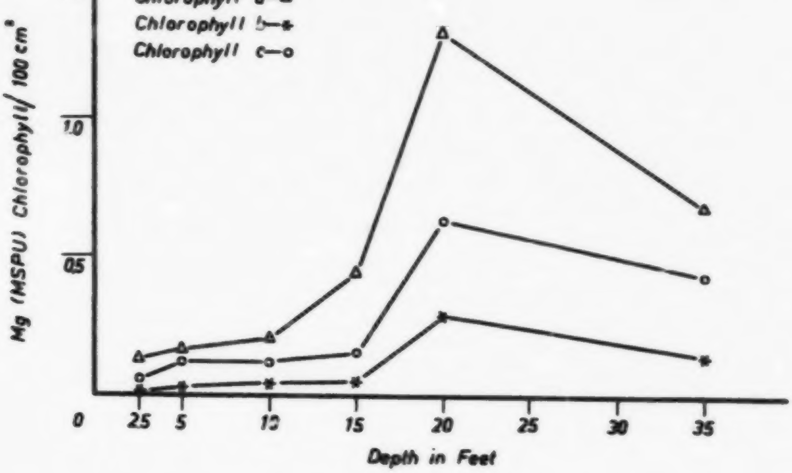

Figure 139. Periphyton Chlorophyll Concentrations (per unit area) at Standard Depths, Beaver Bay, Lake Superior, August 29, 1967.

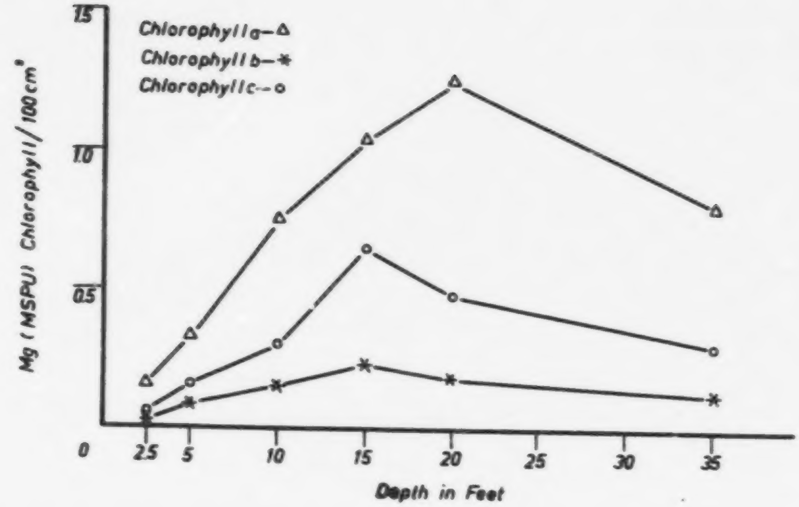

Figure 140. Periphyton Chlorophyll Concentrations (per unit area) at Standard Depths, Beaver Bay, Lake Superior, September 14, 1967.

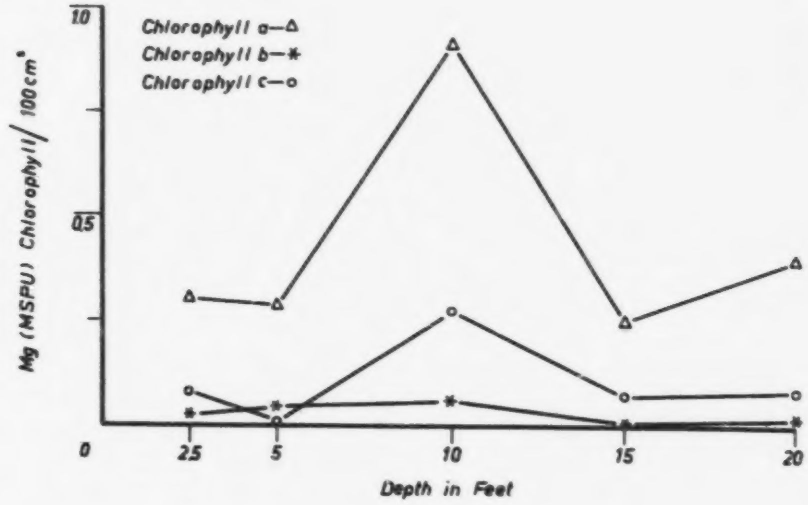

Figure 141. Periphyton Chlorophyll Concentrations (per unit area) at Standard Depths, No-Name Bay, Lake Superior, September 1, 1967.

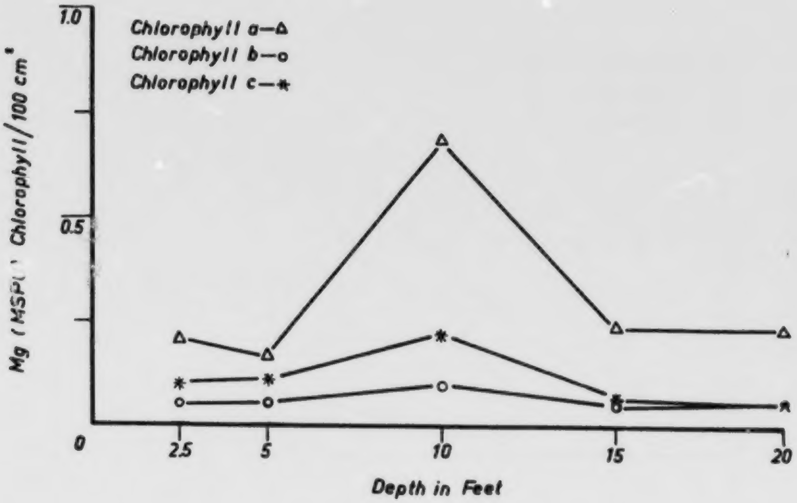

Figure 142. Periphyton Chlorophyll Concentrations (per unit area) at Standard Depths, No-Name Bay, Lake Superior, September 14, 1967.

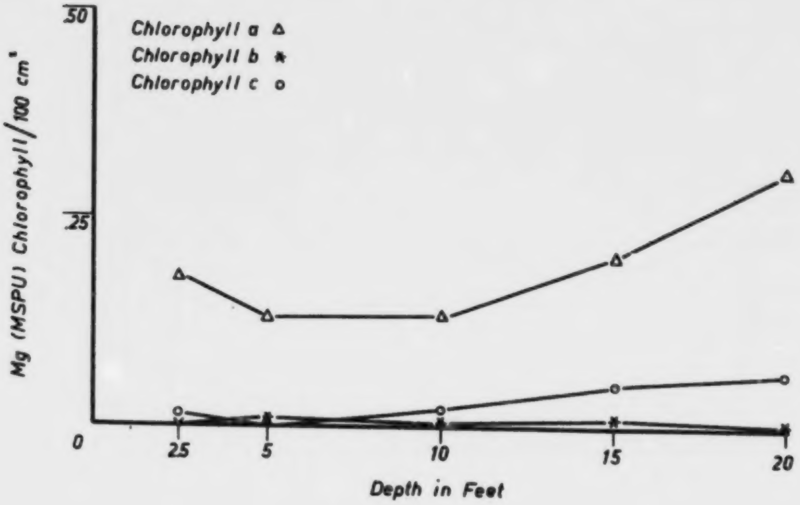

Figure 143. Periphyton Chlorophyll Concentrations (per unit area) at Standard Depths, Sugar Loaf Cove, Lake Superior, August 31, 1967.

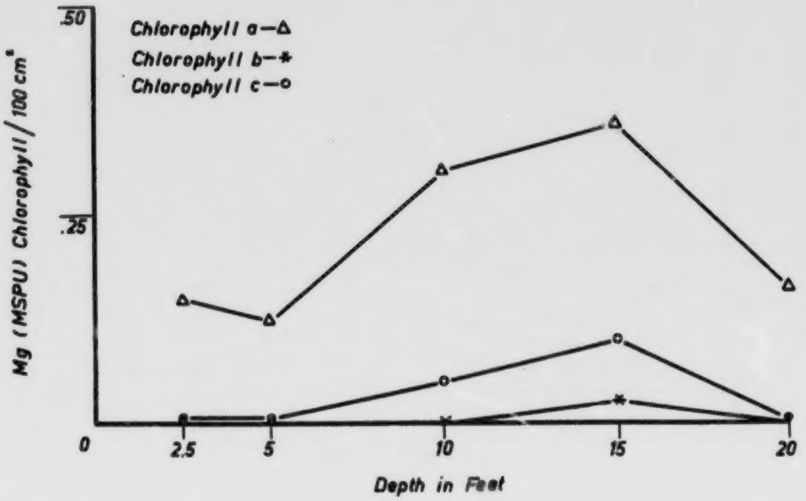

Figure 144. Periphyton Chlorophyll Concentrations (per unit area) at Standard Depths, Sugar Loaf Cove, Lake Superior, September 7, 1967.

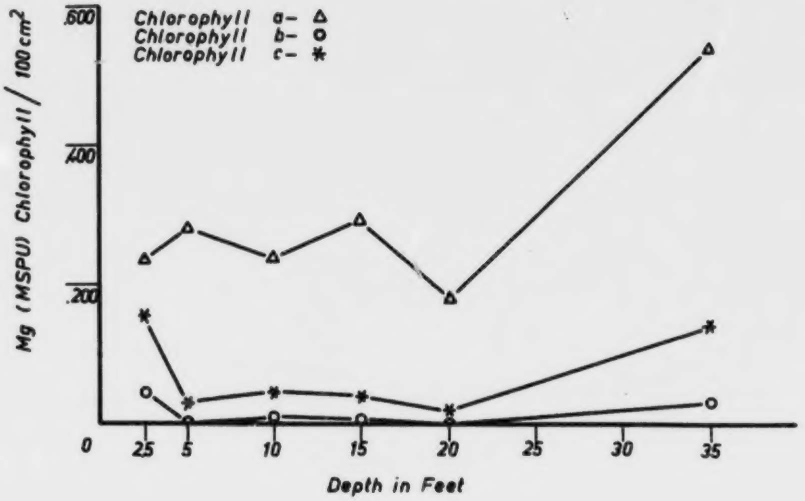

Figure 145. Periphyton Chlorophyll Concentrations (per unit area) at Standard Depths, Tofte Station, Lake Superior, August 31, 1967.

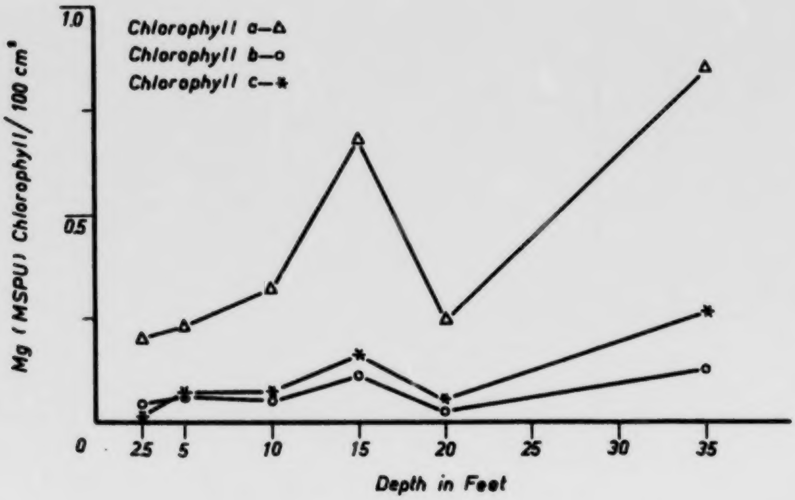

Figure 146. Periphyton Chlorophyll Concentrations (per unit area) at Standard Depths, Tofte Station, Lake Superior, September 7, 1967

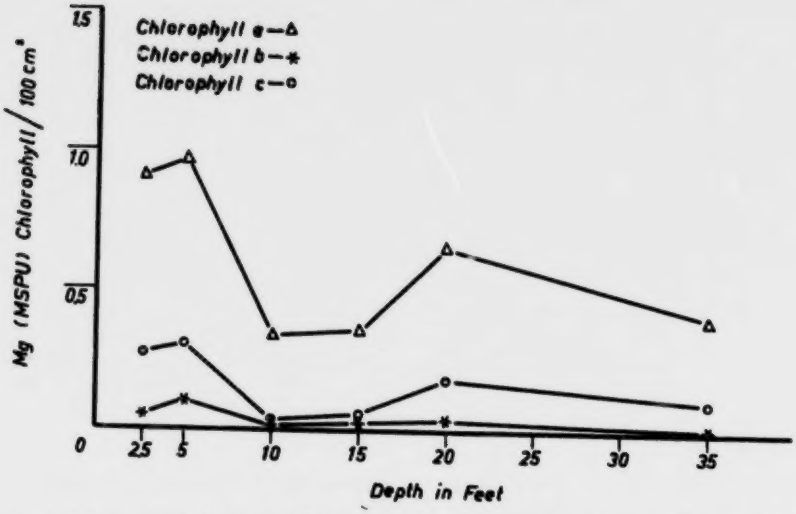

Figure 147. Periphyton Chlorophyll Concentrations (per unit area) at Standard Depths, Lutsen Station, Lake Superior, August 31, 1967.

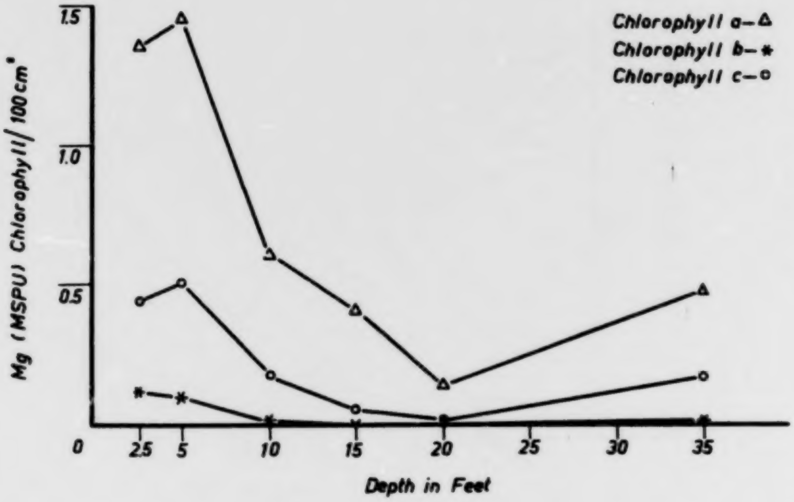

Figure 148. Periphyton Chlorophyll Concentrations (per unit area) at Standard Depths, Lutsen Station, Lake Superior, September 7, 1967.

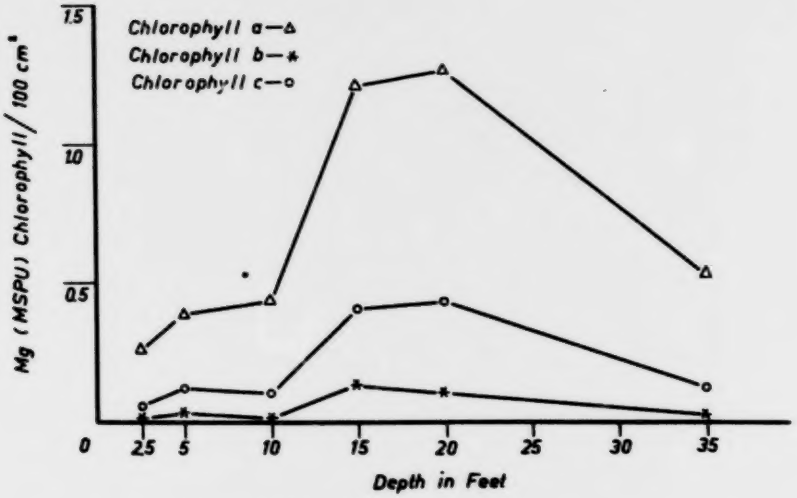

Figure 149. Periphyton Chlorophyll Concentrations (per unit area) at Standard Depths, Good Harbor Bay, Lake Superior, August 31, 1967.

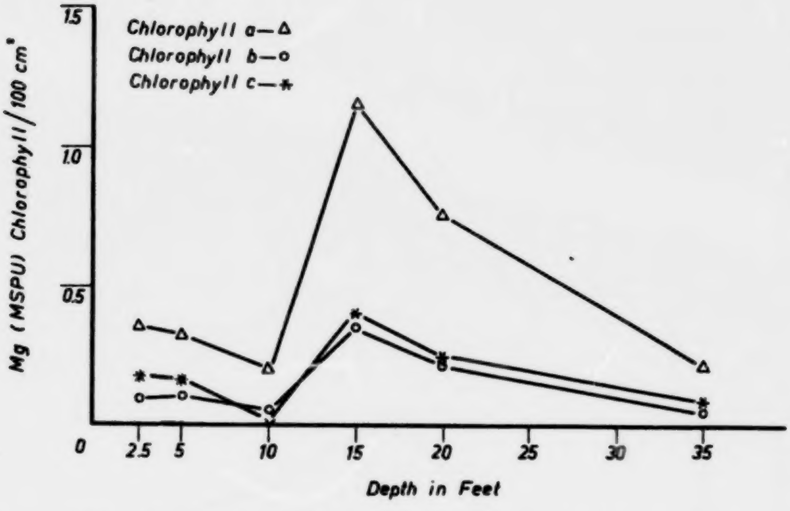

Figure 150. Periphyton Chlorophyll Concentrations (per unit area) at Standard Depths, Good Harbor Bay, Lake Superior, September 7, 1967.

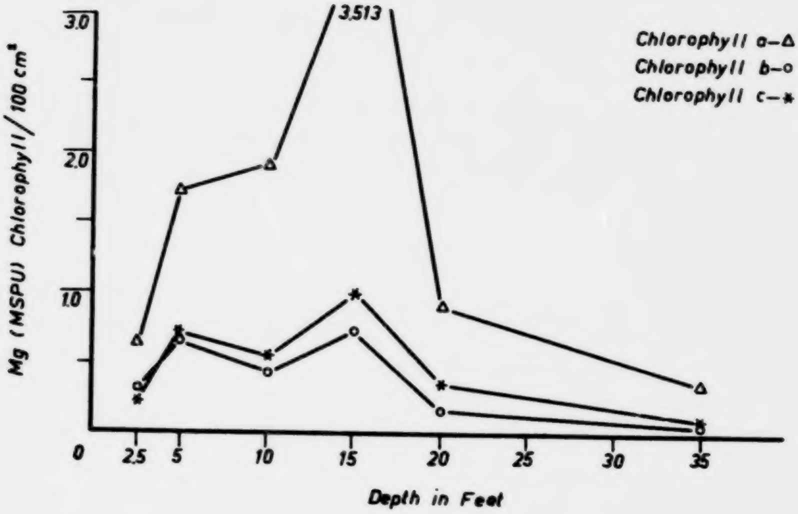

Figure 151. Periphyton Chlorophyll Concentrations (per unit area) at Standard Depths, Grand Marais Station, Lake Superior, August 31, 1967.

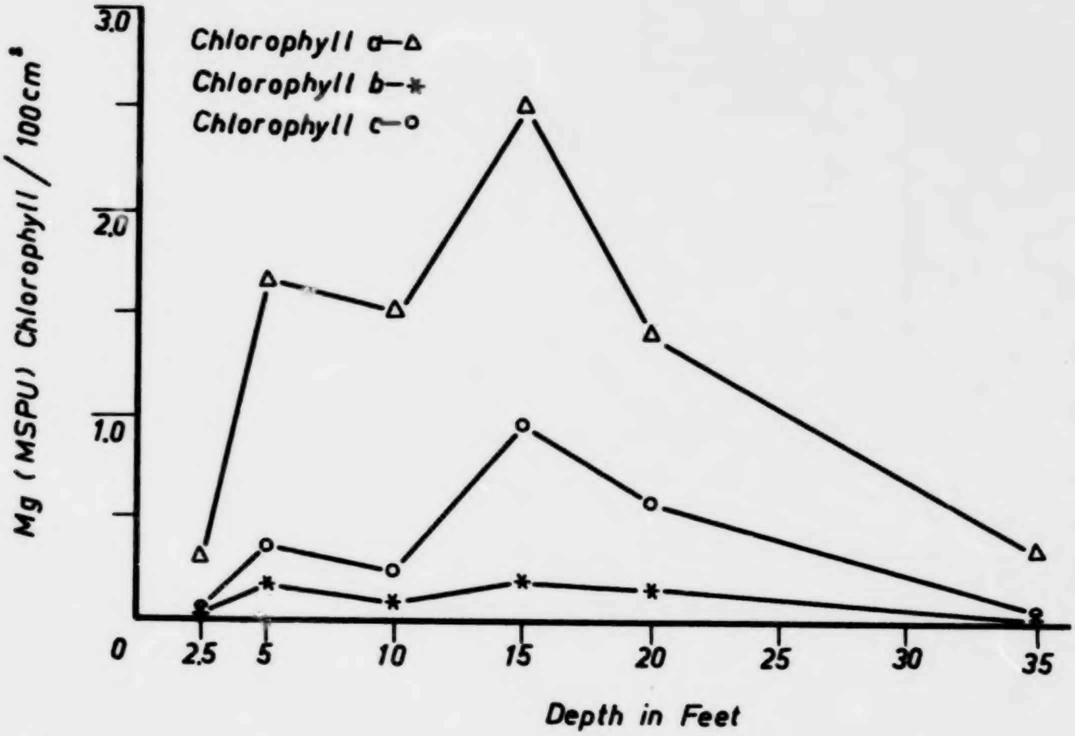

Figure 152. Periphyton Chlorophyll Concentrations (per unit area) at Standard Depths, Grand Marais Station, Lake Superior, September 7, 1967.

Findings in 1968.

The amount of periphyton biomass along the north shore of Lake Superior was well documented by the 1967 data, and the relationships between some of the parameters used to measure the biomass were clarified as a result of the 1967 investigation, However, several questions relating to the biodynamics of this community remained. Biodynamics as used here refers to that combination of internal and external factors which governs the rate and efficiency of energy transfer through a biological system. Since there seemed to be an inverse relationship between light intensity and the concentration of pigments in the organisms, it was necessary to determine experimentally whether or not the concentrations would actually change if light intensity were altered. If such a change occurred, the rate of change could be measured. This factor is important in the consideration of the effects of varying turbidity in lake water on the photosynthetic activity of periphyton.

Although photosynthetic rates for the periphyton had been determined in 1967, these measurements were made under standard conditions of light intensity and temperature, and could not be applied directly to the community in the lake. It had been shown that the photosynthetic efficiency of the pigment unit under standard conditions depended on the depth from which the sample was taken. Therefore, in order to calculate the actual production rates under the variety of conditions to which the periphyton organisms are subjected, it was necessary to determine photosynthetic rates of periphyton in a crossed gradient of light intensity and temperature after the organisms had been "conditioned" to a particular set of conditions. Besides facilitating the adjustment of data collected under standard laboratory conditions in 1967, the 1968 experiments produced basic information about the effects of environmental changes on the periphyton of western Lake Superior.

Analysis of Test Communities and Water Chemistry

Periphyton samples were taken from Stony Point Bay during the summer of 1968 for "conditioning" in the laboratory. For the results of the experiments to be meaningful, it was imperative that the species composition of the sample remain constant throughout the summer. Therefore, the periphyton organisms from a depth of 2.5 feet in Stony Point Bay, where most of the samples were taken for incubation, were counted and identified on nine occasions during the summer of 1968. The results of those counts (Table XXXII) show that the species composition of the samples remained quite constant during the period of testing. The relative numbers of the ten most predominant organisms did not vary significantly. As in previous years, the community was dominated by *Achnanthes microcephala*, *Synedra acus*, and several species of *Navicula*. Thus it was concluded that, for practical purposes, results of experimentation at all times during the summer were comparable and that these results could be employed for adjustment of data collected in 1967.

On one occasion, a sample was taken from Lake Superior near the mouth of the Lester River. The periphyton at this point included a large percentage of *Cladophora*. For the purpose of further establishing the nature of the two communities used in the experiments, photosynthetic rates were determined for samples of each at a variety of temperatures (see Figure 153). There was no sharply defined optimum temperature for photosynthesis in either community; the photosynthetic rate for the Stony Point Bay sample reached a plateau which ranged from 20° to 25° C., while the optimum rate in the sample from the Lester River station was maintained from 20° to 30° C.

Since water from Stony Point Bay was used as the medium for sustaining growth of periphyton in the incubators, it was necessary to show that the quality of the water did not change appreciably during the course of the experiments. The results of chemical analyses which were performed on the water during the summer are presented in Table XXXIII. Techniques described in *Standard Methods for the Examination of Water* and Wastewater (A.P.H.A., 1965) were employed in the chemical analysis of water samples. It is apparent that the water quality did not change significantly throughout the period of experimentation. With this fact established, it was possible to determine experimentally the effects of short-term changes in light intensity and temperature on the productivity of Lake Superior periphyton.

Light Intensity and Chlorophyll Concentrations.

The first series of experiments was designed to demonstrate that the periphyton organisms of Stony Point Bay actually alter their concentration of chlorophyll in response to changes in light intensity, and to determine the rate at which such an alteration occurs. Six rocks supporting the growth of periphyton were taken from a depth of 2.5 feet in Stony Point Bay, where the light intensity was about 5000 foot-candles at mid-day. Six rocks were also taken from a depth of thirty-five feet, where the light intensity was about 100 foot-candles. The amount of total chlorophyll per milligram of ash-free dry weight in the 2.5 and thirty-five foot samples was shown to be 0.00571 milligrams and 0.00916 milligrams, respectively, Three of the rocks from 2.5 feet were then incubated at a light intensity of eighty foot-candles and a temperature of 10° C. The rocks from the thirty-five foot depth were similarly divided and incubated under the same two sets of conditions. At two day intervals, a portion of the periphyton from each rock in each incubator was removed for pigment analysis.

The results of the pigment analyses are presented in Figure 154. The amount of chlorophyll per unit of organic weight in the periphyton which had been accustomed to a light intensity of 5000 foot-candles, but incubated at only 80 foot-candles, began to increase within the first two-day period. The maximum level was reached within six days. During the six-day period, the amount of chlorophyll in the periphyton increased at a rate of 0.00043 mg./mg. of ash-free dry weight/day, or 7.5 per cent/day. The final chlorophyll concentration was 45 per cent higher than the original level. On the other hand, when samples accustomed to 5000 foot-candles were incubated for twelve days at 800 foot-candles, the amount of chlorophyll in the organisms was not altered. Apparently the light intensity must be reduced to some point below 800 foot-candles before the organisms respond by increasing their pigments.

TABLE XXXII

TEN MOST COMMONLY OCCURRING PERIPHYTON ORGANISMS
STONY POINT BAY, 2.5 FOOT DEPTH, 1968
NUMBER (1000's) PER SQUARE CENTIMETER OF ROCK SURFACE

Organism	Date 7-29	 7-31	 8-6	 8-8	 8-12	 8-14	 8-20	 8-27	 9-5
Synedra acus	1,390	1,464	1,080	1,440	1,120	946	858	880	765
Achnanthes microcephala	846	890	660	786	832	786	574	428	460
Navicula spp.	794	644	684	794	540	465	480	386	324
Cymbella spp.	166	120	104	95	144	176	145	96	92
Gomphonema spp.	72	60	66	58	46	40	58	42	38
Synedra ulna	13	6	19	10	16	5	10	12	9
Cocconeis spp.	8	10	12	14	18	12	14	8	10
Denticula thermalis	6	6	3	1	2	4	6	4	4
Fragilaria capucina	8	6	5	6	2	2	6	5	3
Amphora ovalis	2	1	4	4	1	2	1	1	1

TABLE XXXIII

SUMMARY OF WATER CHEMISTRY, STONY POINT BAY, 1968

	Date								
Analysis	7-29	7-31	8-6	8-8	8-12	8-14	8-20	8-27	9-5
Temperature (Degrees C.)	6.9	6.7	12.5	13.2	8.2	5.5	10.2	9.9	13.2
pH	7.76	7.69	7.88	7.84	7.86	7.85	8.07	8.15	7.88
Hardness (mg/L as $CaCO_3$)	49.3	47.5	49.7	47.4	49.4	50.8	50.8	52.3	46.0
Alkalinity (mg/L as $CaCO_3$)	43.3	42.4	41.9	42.4	43.0	42.3	42.5	43.2	42.6
Dissolved solids (mg/L)	58.0	56.0	52.2	64.5	66.5	68.6	60.6	56.4	53.7
Total Phosphorus (mg/L)	<0.05	<0.05	<0.05	<0.05	<0.05	<0.05	<0.05	<0.05	<0.05
Nitrate Nitrogen (mg/L)	0.118	0.118	0.210	0.135	0.121	0.128	0.162	0.159	0.195
Dissolved Oxygen (mg/L)	12.7	12.5	11.3	11.2	12.4	12.6	10.9	11.3	10.5
Dissolved Oxygen (% sat.)	105	106	110	107	108	103	102	103	104
Free Carbon Dioxide (mg/L)	2.10	2.20	1.30	1.45	1.62	1.70	1.00	0.85	1.29

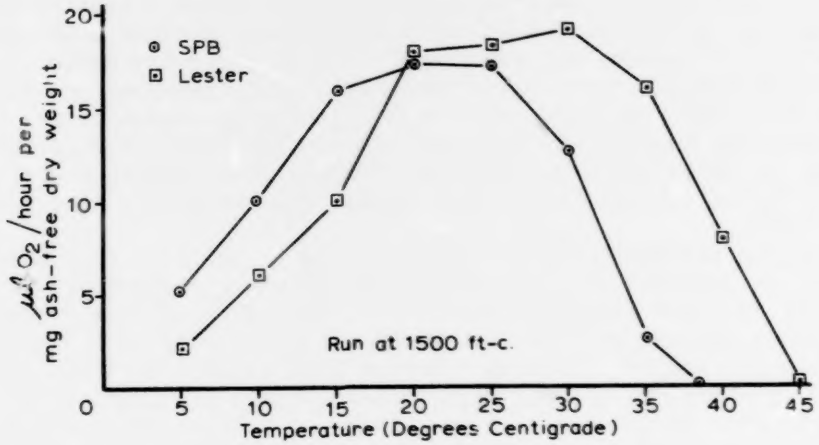

Figure 153. **Photosynthetic Rates of Periphyton From Stony Point Bay and Lester River Station at Various Temperatures, June, 1968.**

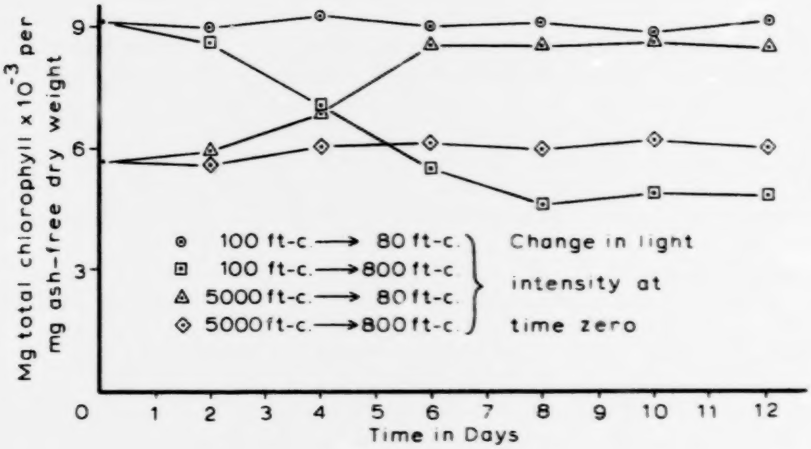

Figure 154. **Change in Periphyton Chlorophyll Concentration (per unit ash-free dry weight) as Light Intensity is Severely Altered.**

The periphyton organisms accustomed to a light intensity of 100 foot-candles, but incubated at 800 foot-candles, decreased the amount of their total chlorophyll continually for an eight-day period. The decrease averaged 0.00058 mg. of chlorophyll/mg. ash-free dry weight/day, or 12.7 per cent/day. The final chlorophyll concentration was forty-nine per cent of the original value. The level of chlorophyll in the samples which had been switched from 100 foot-candles to 80 foot-candles did not change appreciably during the twelve-day test period.

Having established that a light intensity of less than 800 foot-candles was required to stimulate the addition of chlorophyll in the algal cells of Stony Point Bay periphyton, the next step was to determine the maximum intensity at which such an addition would be induced. For this purpose, twelve periphyton samples were taken from Stony Point Bay at a point where the mid-day light intensity was 825 foot-candles. The rocks were divided into groups of three, and the chlorophyll concentration per unit of organic dry weight was determined for each group. Each group of rocks was incubated at 10° C., but at a different light intensity (100, 250, 400 or 600 foot-candles). The amount of chlorophyll per unit of ash-free dry weight was determined for each group of samples at two-day intervals (see Figure 155). The organisms which had been subjected to a reduction in light intensity from 825 foot-candles to 100 foot-candles increased the concentration of their chlorophyll by a total of fifty-five per cent during an eight-day period, after which the concentration remained unchanged for another four days. The daily rate of increase was approximately 6.9 per cent. The samples whose light intensity had been reduced from 825 foot-candles to 250 foot-candles also increased their level of chlorophyll, but to a lesser degree than did the samples incubated at 100 foot-candles. In this case, the increase totaled thirty-six per cent, or 3.6 per cent per day over a ten-day period. The reduction from 825 to 400 foot-candles brought about a total increase in chlorophyll of eighteen per cent over an eight-day period, or 2.25 per cent per day. There was virtually no response to the decrease in light intensity from 825 to 600 foot-candles.

These experiments indicate that the light intensity must be reduced to a point somewhere between 400 and 600 foot-candles before "light-adapted" periphyton organisms will react by adding chlorophyll to their cellular material. Below 400 foot-candles, a nearly linear, inverse relationship exists between light intensity and amount of chlorophyll per unit of organic weight after equilibrium has been reached. Up to this point in the experimentation, it had been shown only that separate "light adapted" or "shade adapted" samples could be stimulated to increase or decrease their pigment concentration by changing the light intensity to which they were exposed. It was necessary to determine whether or not a single sample would respond to decreased light intensity and then to increased intensity. A sample was taken from shallow water in Stony Point Bay (about 5000 ft-c. at mid-day) and placed in an incubator at a light intensity of eighty foot-candles. After twelve days, the light intensity was changed to 800 foot-candles. The amount of total chlorophyll per unit of ash-free dry weight was determined every two days.

Figure 156 shows that the chlorophyll concentration increased for about six days in response to the lowered light intensity, whereupon the concentration remained at the same level for the next six days. When the light intensity was then increased from 80 to 800 foot-candles, the amoun of pigment per unit of organic weight began to fall back toward the original level. After eight days at the high light intensity, the chlorophyll level had returned to a point only slightly higher than that maintained at an intensity of 5000 foot-candles. Thus it has been shown that the periphyton respond quite rapidly to changes in light intensity (between 80 and 800 foot-candles) with virtually no lag phase in the alteration of chlorophyll concentration.

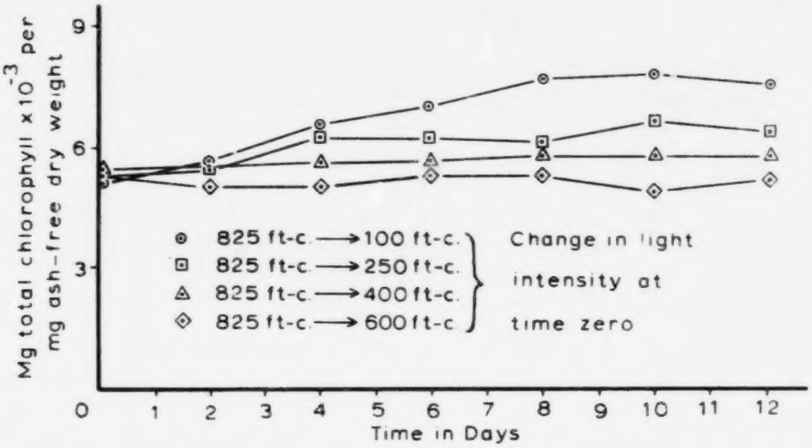

Figure 155. Change in Periphyton Chlorophyll Concentration (per unit ash-free dry weight) as Light Intensity is Moderately Altered.

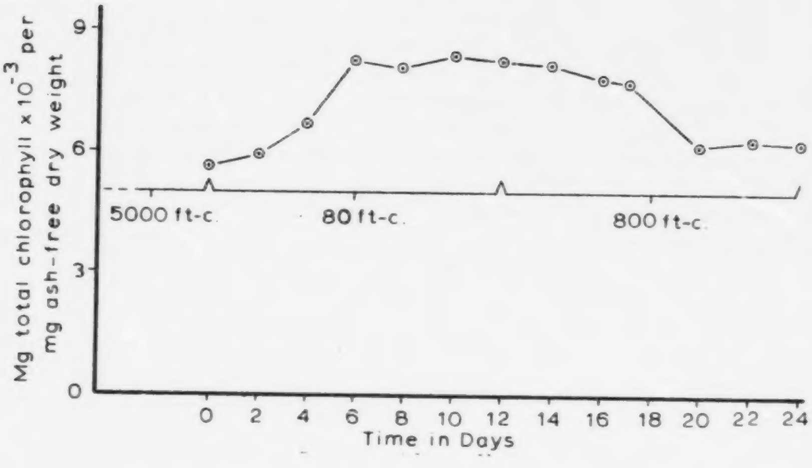

Figure 156. Change in Periphyton Chlorophyll Concentration (per unit ash-free dry weight) as Light Intensity is Reduced and Subsequently Increased.

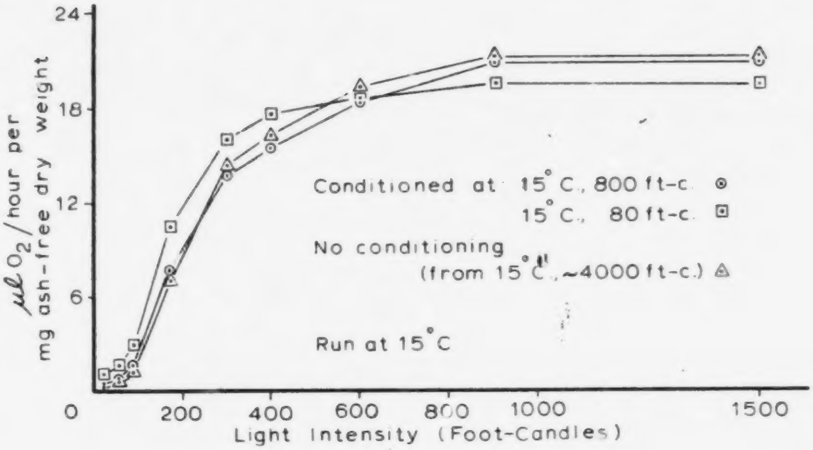

Figure 157. Rate of Photosynthesis in "Conditioned" Stony Point Bay Periphyton at Nine Light Intensities; Samples Conditioned at 80 and 800 Foot-Candles; Run at 15° C.

Conditioned Periphyton Experiment

Six rocks supporting the growth of periphyton organisms were collected from a depth of 2.5 feet in Stony Point Bay, where the light intensity at the time of sampling was about 4000 foot-candles and the temperature 15° C. A portion of this non-conditioned periphyton was removed from each rock and combined for the determination of photosynthetic rate at 15° C. and nine light intensities. The rocks were then divided into two groups and placed in the incubators. One incubator was set at a temperature of 15° C. and light intensity of 800 foot-candles; the other was set at 15° C. and 80 foot-candles. After seven days, the rocks were removed and the organisms tested for photosynthetic rate at 15° C. and nine light intensities. Figure 157 shows that conditioning at 800 foot-candles did not alter the pattern of photosynthetic rate with respect to light intensity from that exhibited by the samples accustomed to 4000 foot-candles. However, the organisms conditioned at 80 foot-candles reached light saturation at a lower intensity than did the other samples. Light saturation as used here may be defined as the point at which the photosynthetic rate is no longer increased significantly in response to increased light intensity. It may also be seen that the sample conditioned at 80 foot-candles produced a higher photosynthetic rate from 20 to 400 foot-candles than the other samples; on the other hand, the maximum rate for the "shade adapted" periphyton (80 ft-c.) was lower than that for the "light adapted" (800 and 4000 ft-c.).

Having shown that the periphyton organisms would adapt to short term changes in light intensity, an experiment was designed to test for adaptation to combinations of light intensity and temperature. Twelve rocks supporting the growth of periphyton were taken from a depth of 2.5 feet in Stony Point Bay. The rocks were divided into groups of three and placed in the four incubators. One incubator was set at 20° C. and 800 foot-candles, one at 10° C. and 80 foot-candles. The samples were incubated in water from Stony Point Bay for ten days. At the end of the test period, the samples were removed and processed as usual. Pigment analyses were run on the four samples and reported in terms of amount of pigment per unit of ash-free dry weight. Aliquots of the same samples were used for the determination of gross photosynthetic rate in crossed gradients of light intensity and temperature.

The results of the photosynthetic rate determinations are presented in Figures 158 through 161. The same general pattern of "shade adapted" and "light adapted" photosynthetic rates seen in the preliminary experiment is exhibited, whether the rates were determined at 10°, 15°, or 20° C. At these temperatures, the samples conditioned at 80 foot-candles produced more oxygen at the lower light intensities than did those conditioned at 800 foot-candles regardless of the conditioning temperature. The samples conditioned at 800 foot-candles, however, reached a higher maximum rate of photosynthesis at light saturation than did those conditioned at 80 foot-candles. Slight differences due to temperature adaptation are also apparent in samples run at 10°, 15°, and 20° C. When run at 20° C. (Figure 158), the photosynthetic rate at light saturation was higher for those samples conditioned at 10° C. The reverse was true when the samples were run at 15° C. (Figure 159) and 10° C. (Figure 160). When the photosynthetic rates were determined at 5° C. (Figure 161), adaptation to temperature was more evident than adaptation to light intensity. The samples conditioned at 10° C. produced the same light-saturated photosynthetic rate at 5° C. regardless of the light intensity to which they were accustomed. Both of the samples conditioned at 10° C. exhibited a higher photosynthetic rate at all light intensities than either of the samples conditioned at 20° C. The compensation point varied somewhat for the different samples, but usually fell between 80 and 130 foot-candles. Compensation point is here defined as the light intensity at which gross photosynthetic rate and respiration rate are equal (net photosynthetic rate = 0).

In order to illustrate another point, the same data were graphed in a different manner (Figures 162 through 163). These graphs show the effects of temperature on the production rates of each sample at the various light intensities. It is apparent that the test temperatures produced a wider spread in the photosynthetic rates in the samples incubated at 20° C. than in the ones incubated at 10° C. Samples conditioned at 20° C. produced more oxygen when run at 20° C. and less when run at 5° C. than those conditioned at 10° C. This point is emphasized by the temperature coefficients (Q_{10}) which were calculated for all of the samples. Q_{10} calculated for the temperature range of 5° C. to 20° C. for samples incubated at 20° C. and 800 foot-candles was about 2.0 at light saturation; the value for samples incubated at 20° and 80 foot-candles was about 2.5 at light saturation. In contrast, Q_{10} for samples incubated at 10° C. and 800 foot-candles was approximately 1.7 at light saturation, while the value for samples incubated at 10° C. and 80 foot-candles was about 1.5. Q_{10} was also calculated for all samples at all test light intensities for three intermediate temperature ranges (5° - 10° C., 10° - 15° C., 15° - 20° C.). These values are more variable than the ones calculated for the larger temperature range, especially at the lower light intensities.

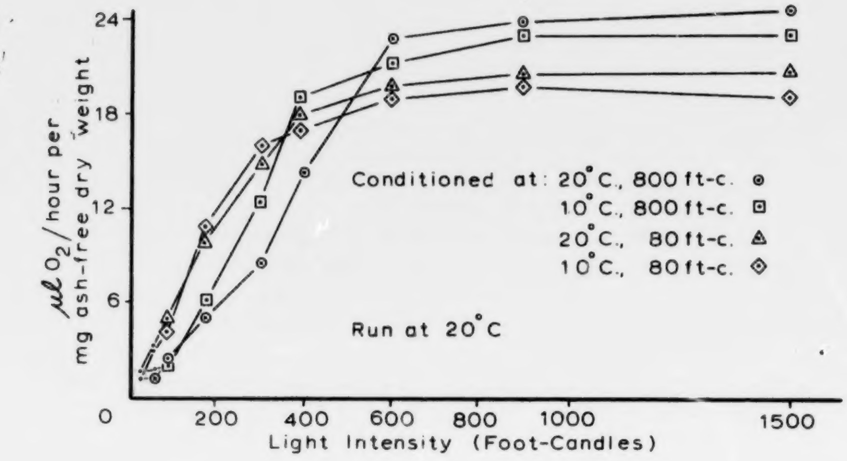

Figure 158. **Rate of Photosynthesis in "Conditioned" Stony Point Bay Periphyton at Nine Light Intensities; Run at 20° C.**

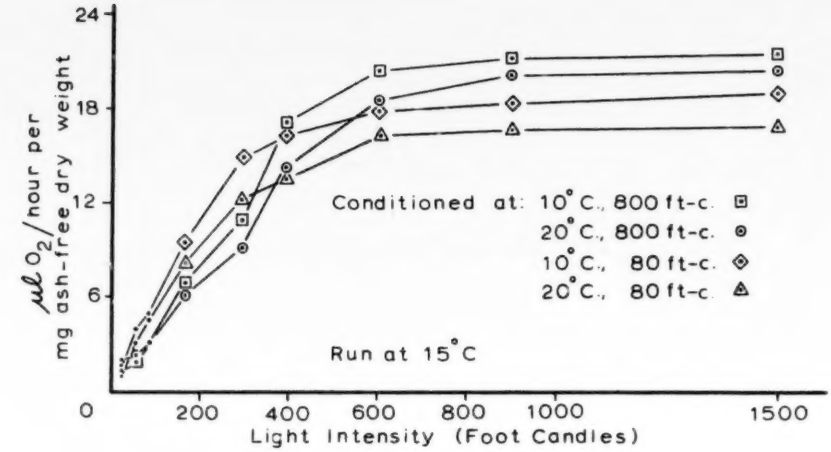

Figure 159. **Rate of Photosynthesis in "Conditioned" Stony Point Bay Periphyton at Nine Light Intensities; Run at 15° C.**

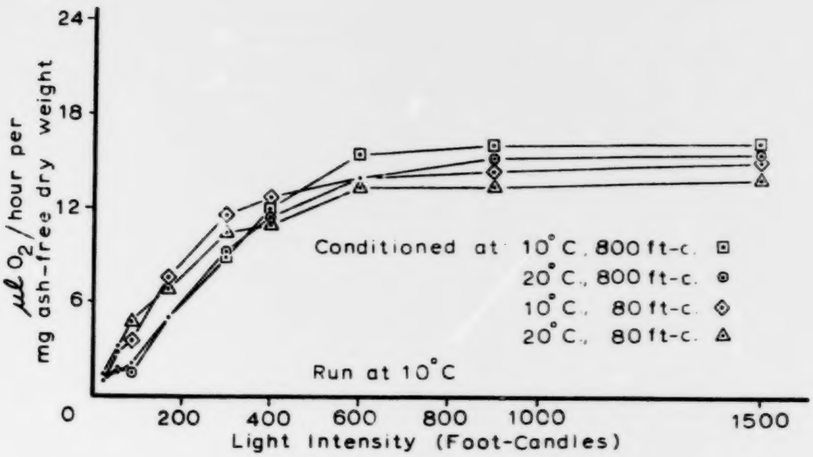

Figure 160. Rate of Photosynthesis in "Conditioned" Stony Point Bay Periphyton at Nine Light Intensities; Run at 10° C.

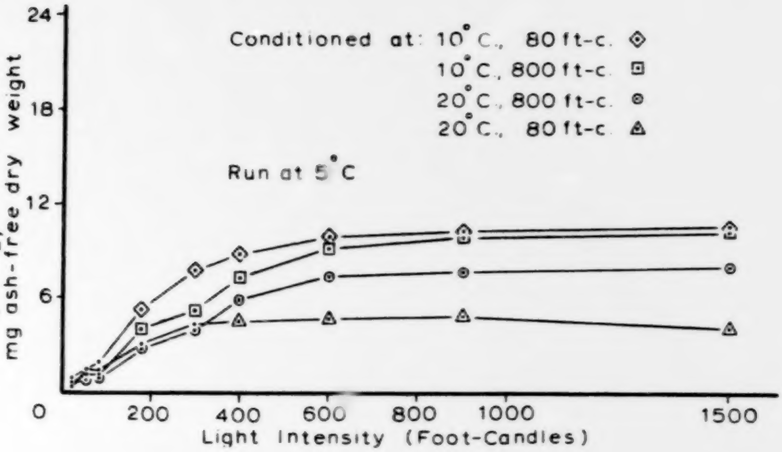

Figure 161. Rate of Photosynthesis in "Conditioned" Stony Point Bay Periphyton at Nine Light Intensities; Run at 5° C.

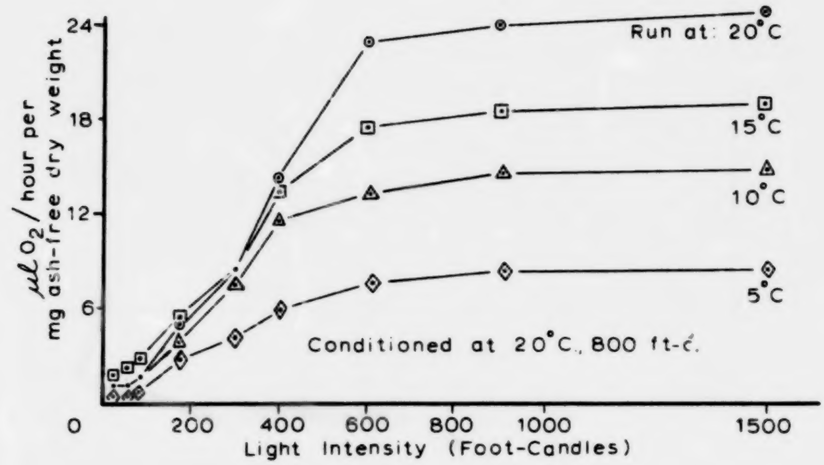

Figure 162. Rate of Photosynthesis in Stony Point Bay Periphyton at Nine Light Intensities and Four Temperatures; "Conditioned" at 20° C., 800 Foot-Candles.

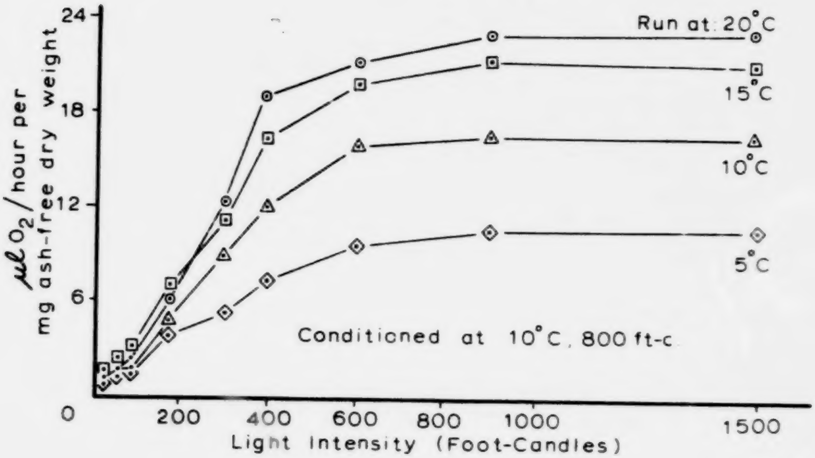

Figure 163. Rate of Photosynthesis in Stony Point Bay Periphyton at Nine Light Intensities and Four Temperatures; "Conditioned" at 10° C., 800 Foot-Candles.

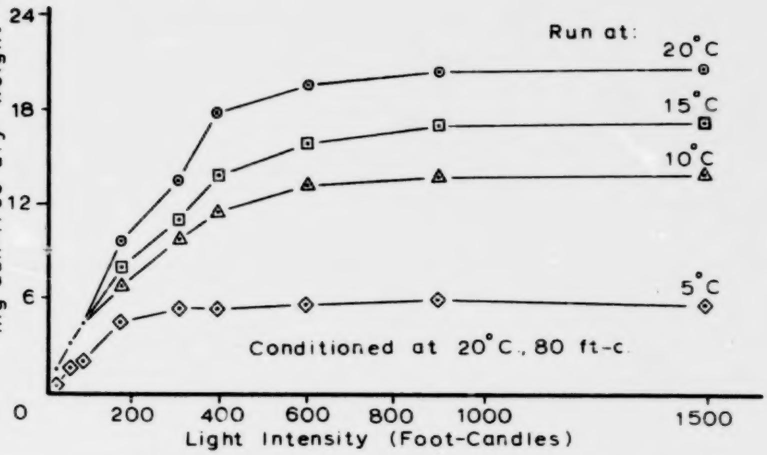

Figure 164. Rate of Photosynthesis in Stony Point Bay Periphyton at Nine Light Intensities and Four Temperatures; "Conditioned" at 20° C., 80 Foot-Candles.

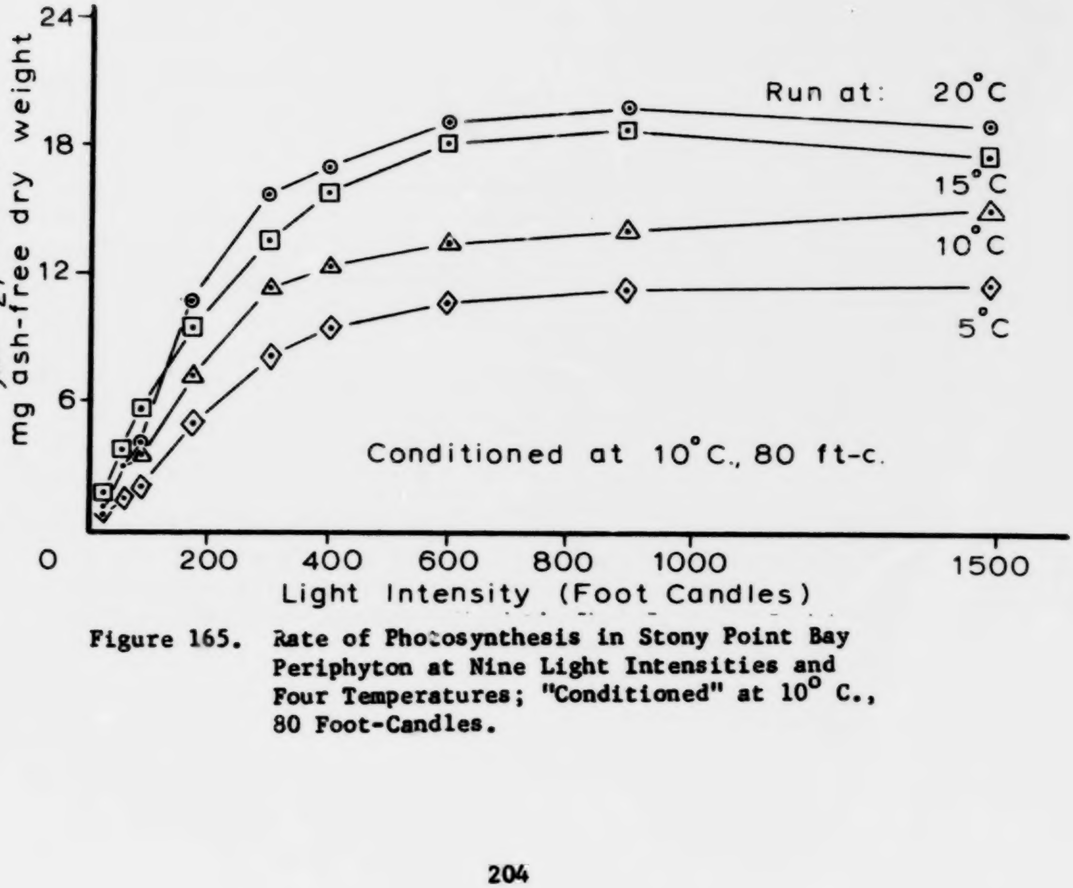

Figure 165. Rate of Photosynthesis in Stony Point Bay Periphyton at Nine Light Intensities and Four Temperatures; "Conditioned" at 10° C., 80 Foot-Candles.

Assimilation values were calculated for the four samples at all light intensities and temperatures. The assimilation values at all test light intensities are higher for samples incubated at 800 foot-candles than for those incubated at 80 foot-candles, regardless of temperature, even though the latter samples had more chlorophyll per unit weight. This fact confirms the suggestion, first made in 1966, that the chlorophyll unit becomes less efficient as an organism adds more chlorophyll to its cellular material.

Following the conclusion of the experiment, the entire procedure was repeated, the only difference being that the samples were collected from a depth of thirty-five feet in Stony Point Bay instead of from 2.5 feet. The purpose of the second experiment was to determine whether or not samples accustomed to relatively low light intensity and temperature would be affected by conditioning in the same manner as were those from an area of high light intensity and temperature. The photosynthetic rates measured in crossed gradients of light intensity and temperature indicate that the samples from thirty-five feet reacted to the conditioning in the same way as did the samples from 2.5 feet.

In order to determine the effects of conditioning periphyton samples at intermediate light intensities, samples were collected from a depth of fifteen feet in Stony Point Bay (825 foot-candles at midday; 15° C.) and incubated for ten days at 100, 250, 400, and 600 foot-candles and a temperature of 15° C. Photosynthetic rates were then determined for the four samples at nine light intensities and four temperatures. The "shade" reaction was obvious in the rates produced by the sample which had been incubated at 100 foot-candles, as light saturation is reached at 300-400 foot-candles. This type of reaction was still present, but less obvious, in the sample incubated at 250 foot-candles. Light saturation in the sample incubated at 400 foot-candles was reached at about 600 foot-candles. The curve produced by plotting photosynthetic rate against light intensity for the sample incubated at 600 foot-candles nearly paralleled that of the original "light adapted" sample.

Since the periphyton community at the Lester River station in Lake Superior was one of the few which differed significantly from the community at Stony Point Bay, photosynthetic rates of a "non-conditioned" sample from that station were determined in crossed gradients of light intensity and temperature. The temperature at the sampling point was 21° C., and the light intensity was about 4500 foot-candles. The purpose was to see whether or not the rates for a community rich in Cladophora would differ from those of the diatom community of Stony Point Bay. The results of this experiment are shown in Figure 166. The general magnitude of the photosynthetic rates, expressed as microliters of oxygen produced per milligram of ash-free dry weight, was very similar to that exhibited by the samples from Stony Point Bay. The slope of the curves was typical of the "light adapted" reaction, and light saturation was reached at about 900 foot-candles.

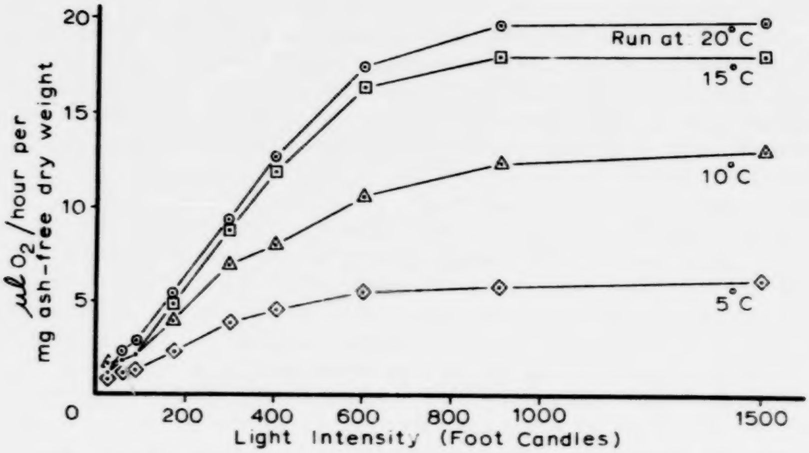

Figure 166. **Rate of Photosynthesis in Periphyton from Lester River Station (Lake Superior) at Nine Light Intensities and Four Temperatures.**

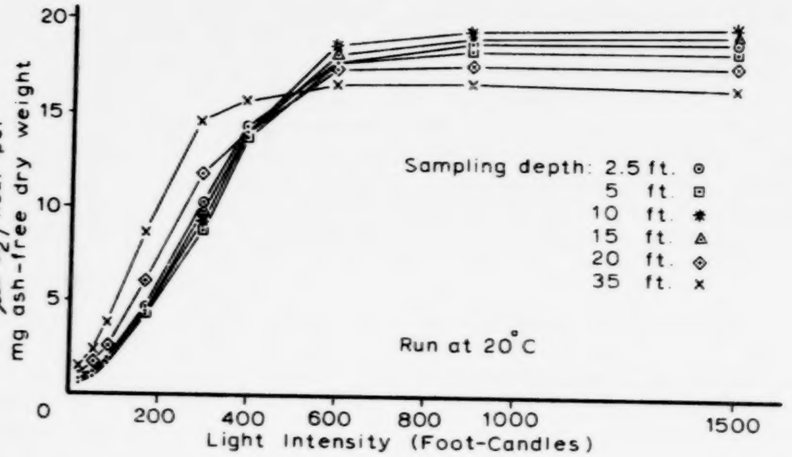

Figure 167. **Rate of Photosynthesis in Stony Point Bay Periphyton from Standard Depths Following Period of Clear Weather; Run at Nine Light Intensities.**

Photosynthetic Rates of Non-conditioned Periphyton

Several samples of Stony Point Bay periphyton were collected from the six standard sampling depths during the summer of 1968 for analysis of photosynthetic rates at various light intensities. One such group of samples was taken on August 9, following a ten-day period of very clear weather. During that period, there was little wave action and very low turbidity in Stony Point Bay. The light intensities at the six standard depths when the samples were taken were as follows:

2.5' - 5250 foot-candles
5' - 4250
10' - 2330
15' - 910
20' - 475
35' - 250

The photosynthetic rates of these samples at nine light intensities are shown in Figure 167. There is little difference in the curves for the samples from 2.5, 5, 10, and 15 feet. These curves are typical of the "light adapted" reaction; light saturation was reached at about 600 foot-candles. The thirty-five foot sample produced photosynthetic rates which were typical of the "shade adapted" reaction, reaching light saturation at about 400 foot-candles. At all intensities below 600 foot-candles, the thirty-five foot sample produced more oxygen per unit of organic weight than the other samples. Above 600 foot-candles, however, it produced less than the others. A hint of the "shade" reaction was exhibited by the sample from twenty feet.

Another group of samples was taken on August 22. During the period between August 13 and August 22, the weather was cloudy and winds caused considerable wave action in Stony Point Bay. Turbidity was relatively high. Light intensities at the standard depths when the samples were collected were as follows:

2.5' - 2440 foot-candles
5' - 1250
10' - 950
15' - 325
20' - 225
35' - 105

Photosynthetic rate curves for these samples were somewhat different than those for samples taken on August 9 (see Figure 168). The 2.5, 5, and 10 foot samples still reacted as "light adapted" communities. However, the curves for samples from all three of the remaining depths exhibited the "shade adapted" reaction, reaching light saturation at about 300 to 400 foot-candles. The periphyton at fifteen and twenty foot depths in the bay were presumably conditioned to lower light intensity during the stormy period. These results show that the adaptations which were induced in the laboratory can occur naturally in the lake.

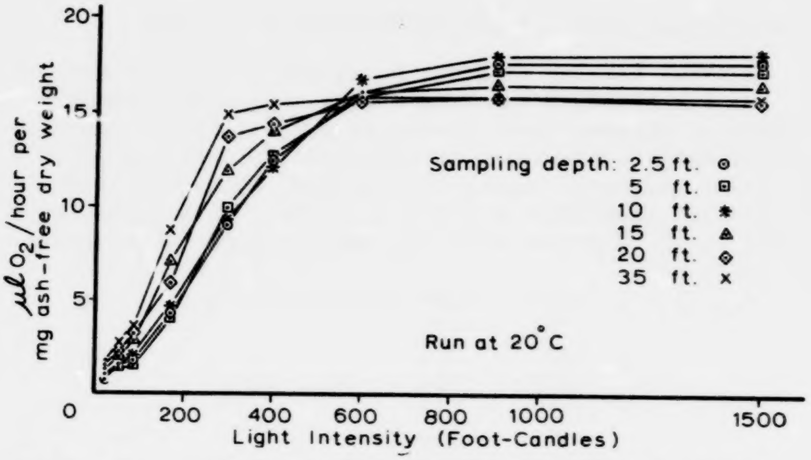

Figure 168. Rate of Photosynthesis in Stony Point Bay Periphyton from Standard Depths Following Period of Stormy Weather; Run at Nine Light Intensities.

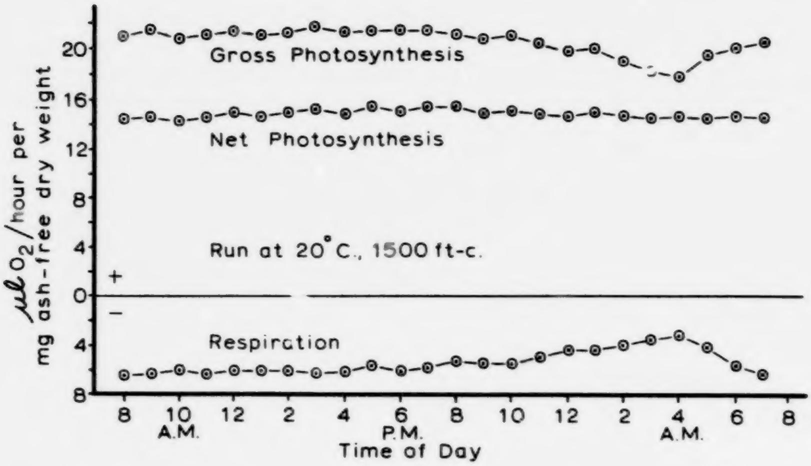

Figure 169. Rate of Periphyton Photosynthesis and Respiration Measured Hourly (24 Hours).

Diurnal Variation in Respiration Rate

For the purpose of calculating daily net production rates from the 1967 periphyton data, it was assumed that the respiration rate remained constant throughout a twenty-four hour period. To test this assumption, a sample from the 2.5 foot depth in Stony Point Bay was tested for respiration rate in the dark at hourly intervals for twenty-four hours. Net photosynthetic rate during alternate light periods was also determined each hour. Gross photosynthetic rate was calculated from net photosynthesis and respiration measurements. The results of these hourly measurements are presented in Figure 169. The net photosynthetic rate remained quite constant during the entire twenty-four hour period. However, the respiration rate and gross photosynthetic rate both decreased during the nighttime hours, reaching minimum values at about 4:00 A. M. Between 10:00 P.M. and 7:00 A.M., the rates averaged lower than the daytime readings by about 2.5 microliters of oxygen/hour/mg. of organic weight. The diurnal reduction in respiration should be taken into account when net daily production rates are calculated from instantaneous rates determined in the daytime. As a point of academic interest, this experiment demonstrated that gross photosynthetic rate should not be measured in artificial light during the nighttime hours, because that rate is not a true reflection of photosynthesis in the daytime.

On another occasion, the same experiment was run using a sample of Stony Point Bay periphyton which had been incubated in constant light (800 foot-candles) for ten days (see Figure 170). In this case, no diurnal variation in respiration rate appeared during the twenty-four hour period. It is assumed that the long period of constant light destroyed the respiratory rhythm.

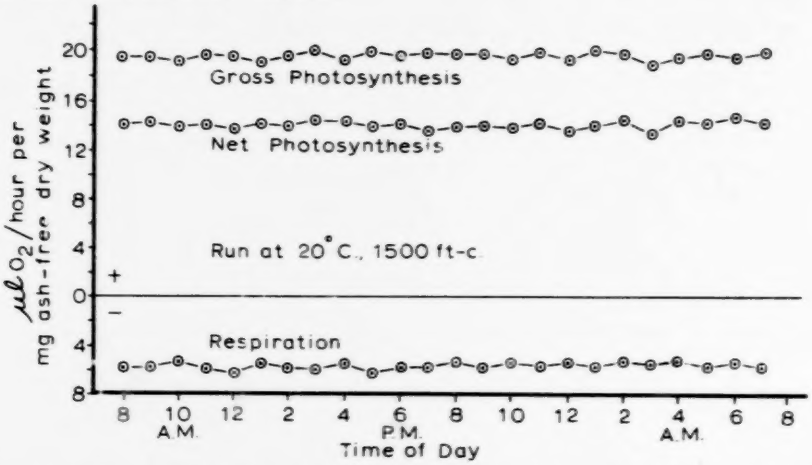

Figure 170. Rate of Periphyton Photosynthesis and Respiration (24 Hours) Following Ten-Day Period of Incubation in Continuous Light.

Alteration of 1967 Photosynthesis Data

The photosynthesis data collected in 1967 under standard laboratory conditions will be useful in comparing the relative production rates of Lake Superior periphyton with those of communities in other bodies of water. If future tests on Lake Superior periphyton are run under the same standard conditions, the results can be used to detect changes in periphyton activity within the lake. However, if these data are to be viewed as a reflection of true production rates at different depths in the lake, alterations must be made to account for the effects of light intensity and temperature.

The calculated average daily variation in light intensity at each of the standard depths during the summer of 1967 is shown in Figure 171. It is obvious that photosynthesis would occur at less than the light-saturated rate for a different length of time at each station. The light intensity data from Figure 171, the temperature data from Table XXVII, and the production rate data have been employed in the conversion of the 1967 rates to those more nearly reflecting conditions in the lake. The result of each measurement made during the first two summers could be altered according to the prevailing conditions at the time of sampling; however, to provide an example of the conversion process, only the mean photosynthetic rates for 1967 will be altered.

The mean gross photosynthetic rate of periphyton from the 2.5 foot depth in Stony Point Bay was 44.6 microliters per hour per square centimeter of rock surface (from Table XXVIII). The respiration rate was 13.9 microliters/hour/cm^2. During thirteen daylight hours, the light intensity at the 2.5 foot depth was at the optimum level or above, so no correction is made for this factor during that period. However, the average temperature at 2.5 feet was 12.5° C. On the basis of the difference between photosynthetic rate at 20° C. and 12.5° C. (interpolated) the rate for those thirteen hours should be reduced by eighteen per cent, to 38.6 microliters/hour/cm^2. For two hours of daylight, both temperature and light intensity (average 600 foot-candles) were below the optimum level. The difference between photosynthetic rate at 20° C. with light saturation, and photosynthetic rate at 12.5° C. with a light intensity of 600 foot-candles, requires a reduction of the measured rate by twenty-four per cent, to 33.9 microliters/hour/cm^2. When these two figures are properly weighted, the hourly rate becomes 36.2 microliters/hour/cm^2, or 543 microliters/cm^2 for a fifteen hour day.

The average 1967 respiration rate for the 2.5 foot samples should be reduced by seven per cent to account for the apparent nighttime variation. The rate must be further reduced by eighteen per cent of the original value to account for the difference in respiration rate at 20° C. and 12.5° C. Thus the value is converted to 10.0 microliters/hour/cm^2. During a twenty-four hour day, the respiration amounts to 240 microliters/cm^2. Therefore, the resultant net photosynthetic rate becomes 303 microliters/day/cm^2, which is gross photosynthetic rate (543) minus respiration rate. This value is equal to a production rate of

1.602 grams of carbon fixed per day per square meter. The true mean production rates for the other five sampling stations were computed in a similar manner, and are presented in Table XXXIV. The amount of reduction, in terms of per cent of the original value, increased considerably with increased sampling depth.

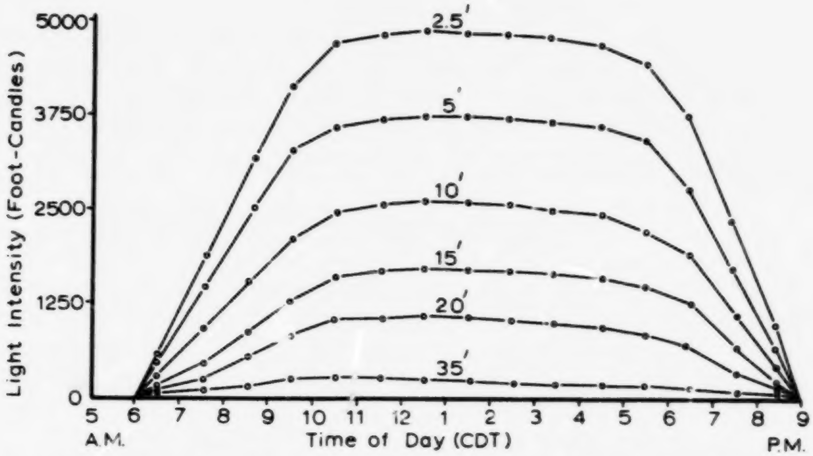

Figure 171. Calculated Hourly Light Intensity at Standard Depths in Stony Point Bay; Average for June - September, 1967.

TABLE XXXIV

PERIPHYTON PRODUCTION RATES CONVERTED TO EXPECTED RATES UNDER NATURAL CONDITIONS, STONY POINT BAY, 1967 GRAMS CARBON FIXED PER DAY PER SQUARE METER

Depth	Measured value under standard lab. conditions*	Calculated value for average lake conditions	% reduction
2.5'	1.79	1.60	10.6
5	1.30	1.12	14.0
10	0.96	0.73	16.6
15	0.63	0.50	21.2
20	0.81	0.58	28.0
35	0.57	0.17	70.2

* Standard laboratory conditions were 20° C and 1500 ft-c.

The corrected photosynthesis data and the light intensity curves can also be used to determine the efficiency of energy utilization by the periphyton of Stony Point Bay during the summer of 1967. If the energy required to form a gram-molecule of glucose is taken to be 676,000 gram-calories and is accompanied by the liberation of 22.4 X 6 liters of oxygen, then one gram-calorie will produce 190 microliters of oxygen. Since the periphyton organisms cover the substrate completely, all of the radiation within the range of 380 to 720 millimicrons reaching a particular depth is available for use in photosynthesis. The light curves in Figure 171 are based on light reception by a selenium cell, which is sensitive only to light in the photosynthetic range (Jerlov, 1966). In that range, one foot-candle is equal to 0.00398 gram-calories/hour/cm^2 (Strickland, 1958). When this conversion has been made, efficiency of energy utilization may be calculated by the use of the following equation.

$$\%\ \text{eff.} = \frac{(\text{net microliters } O_2/\text{day}/\text{cm}^2)\ (100)}{(\text{gram-calories}/\text{hour}/\text{cm}^2)\ (15)\ (190)}$$

Energy reaching the floor of Stony Point Bay during the summer of 1967 averaged 6.65 gram-calories per hour of daylight per square centimeter. Since the average net production rate was 157 microliters of oxygen produced per day per square centimeter, the efficiency of energy utilization was 0.82 per cent. This value compares favorably with the efficiency factor (1%) calculated for phytoplankton in Lake Mendota, Wisconsin, by Juday (1940). On this basis, it is concluded that periphytic algae are capable of utilizing energy as efficiently as the free-floating forms.

Summary and Conclusions
Photosynthetic Pigments and Productivity of Periphyton

The study just described in detail was a comprehensive project designed to measure productivity and explore the biodynamics of Lake Superior periphyton. It was carried out during the summers of 1966, 1967, and 1968. The biomass, community structure, and photosynthetic activity of epilithic periphyton from a representative area, Stony Point Bay, were determined by examination of a variety of parameters. Naturally occurring periphyton and regrowth organisms were studied. In addition, the attached communities of other north shore stations were examined, although to a lesser extent. Data reflecting the effects of certain environmental conditions on the productivity of periphyton were acquired in 1968 by laboratory experimentation. These data were employed in adjusting production rates which had been determined under standard laboratory conditions during the two previous summers. Some of the more important findings and conclusions were:

(1) Pigment concentrations show that the biomass of the periphyton of Lake Superior's north shore is similar in magnitude to other oligotrophic bodies of water. Total pigment concentrations ranged from 0.338 to 3.59 milligrams per 100 square centimeters of rock surface, and averaged 1.36 mg/100 cm^2.

(2) Pigment ratios indicate that most of the north shore periphyton was dominated by organisms of the Phylum Chrysophyta.

(3) Assimilation values for Stony Point Bay periphyton averaged 1.48 grams of carbon fixed per gram of chlorophyll in 1967.

(4) The total standing crop of Stony Point Bay periphyton in terms of dry weight was 55.5 tons, or 156 grams per square meter in 1967.

(5) Regrowth periphyton over a period of forty-six days, was equivalent to approximately one-third only of the biomass of naturally occurring periphyton. Chlorophyll levels increased by an average of 0.00057 grams per square meter per day.

(6) Net production by the periphyton in 1967 averaged 1.01 grams C fixed/M^2/day, or 3.35 grams glucose per M^2/day. The ratio of gross photosynthesis to respiration averaged 3.17.

(7) In water up to forty feet deep in Lake Superior, periphyton can be five to six times as important in primary production as the phytoplankton.

(8) Laboratory experiments showed that alteration of light intensity (below 800 foot-candles) causes a rapid change in the chlorophyll content of the periphyton. The maximum rate of chlorophyll reduction in response to a substantial increase in light intensity was shown to be 12.7 per cent per day for eight days. The

most rapid increase in chlorophyll concentration in response to a severe reduction in light intensity was 7.5 per cent per day for six days.

(9) Short-term "conditioning" of periphyton to different combinations of light intensity and temperature caused a variety of responses when the photosynthetic rate was measured in crossed gradients of light intensity and temperature.

(10) For conditioned samples at light saturation Q_{10} ranged from 1.24 to 2.48. The compensation point varied from 80 to 130 foot-candles.

(11) Naturally occurring periphyton was shown to exhibit typical "light-adapted" or "shade-adapted" photosynthetic reaction depending on the prevailing level of light intensity.

(12) The efficiency of energy utilization by Stony Point Bay periphyton was found to be 0.82 per cent, a typical value for algal communities.

It is believed that the periphyton community will be very useful in the future as an indicator of water quality, and that the data collected in the course of this investigation will provide a baseline for detecting the gradual advance of eutrophication in Lake Superior.

SECTION VII

The Potential of Periphyton as a Source of Plankton Organisms

During the period from July 21 through August 19, 1970, periphyton and phytoplankton of Lake Superior were studied in a miniature replica of their natural environment, using two simulated "lake basins" of natural rock located on the shoreline at Castle Danger and immediately adjacent to the lake. These pools exposed to the same climatic conditions prevailing over the lake in this general area, were furnished with a constant flow of lakewater. Rocks gathered from the lake bottom were placed in these pools to provide a natural substrate for periphytic growth. Periphyton from the control and test pool rocks were collected at regular weekly intervals while the phytoplankton population in both pools and in the lakewater intake was sampled on a bi-weekly basis.

The types of phytoplankton and numbers of organisms per liter found in water samples from the lakewater intake, the control pool effluent and the test pool effluent are summarized in Tables 36 to 38. Comparable counts of the periphyton could not be made directly since quantitation of these attached forms must be on the basis of organisms per square centimeter of rock surface rather than individuals per liter of water flowing through. Although the phytoplankton and periphyton are necessarily expressed in different units and are, therefore, amenable only to direct comparison within each group, their proportionate abundance is nevertheless indicative of analogous and relative magnitudes between organisms in the two populations. Results of the periphyton study are presented in Tables 39 to 41.

For practical purposes it had been decided at the outset that only the most abundant species in each sample would be counted, hence blank spaces in tables referred to do not of necessity mean that a given organism was totally absent on a given day. Instead it simply indicates that not enough individuals of that species were present on that occasion to qualify it as a member of the predominant group. This helps to explain, for example, such occasional anomalies as the fact that both Melosira and Ulothrix were present in samples from the test pool effluent but were never recorded in the intake.

Except for Sphaerotilus, a filamentous alga-like bacterium, all organisms included in the counts were algae. They were divided among the various phyla as follows: thirteen species of Chrysophyta, five species of Chlorophyta and three species of Cyanophyta. The complete list of these organisms, in terms of genera and the types of samples in which they were found, is presented in Table 35.

From this table it will be seen that Chrysophytes constituted the predominant group of organisms in both the periphyton and the phyto-

Table 35
Castle Danger Studies 1970
Predominant Organisms in the Phytoplankton and Periphyton

	Phytoplankton			Periphyton	
	Intake	Control Pool	Test Pool	Control Pool	Test Pool
Chrysophyta					
Achnanthes	x	x	x	x	x
Cymbella	x	x	x	x	x
Fragilaria	x	x	x	x	x
Gomphonema	x	x	x	x	x
Nitzschia	x	x	x	x	x
Synedra	x	x	x	x	x
Dinobryon	x	x	x	-	x
Asterionella	x	x	x	x	-
Tabellaria fenestrata	x	x	x	x	-
Tabellaria flocculosa	x	x	x	-	-
Rhizosolenia	x	x	x	-	-
Melosira	-	-	x	-	-
Denticula	-	-	-	x	-
Cyanophyta					
Oscillatoria	x	x	x	x	x
Lyngbya	x	x	x	-	-
Coccochloris	x	x	x	-	-
Chlorophyta					
Chlamydomonas	x	x	x	x	x
Cylindrocapsa	x	x	x	-	-
Ulothrix	-	-	x	-	x
Staurastrum	-	-	-	x	-
Scenedesmus	-	-	-	-	x
Schizomycophyta					
Sphaerotilus	x	x	x	-	-
Total species	17	17	19	12	11

x = present

- = absent or not sufficiently abundant to list plankton. Eight species, including six diatoms, one Chlorophyte and one Cyanophyte, were found at all five of the sampling sites. This information may be further summarized by tabulating the number of species in each category and the percent this represents of total number of species present.

Summary of Plankton Samples

Phylum	Intake and Control Pool Effluent Species Present	Test Pool Effluent Species Present
Chrysophyta	11 (65%)	12 (63%)
Cyanophyta	3 (17%)	3 (16%)
Chlorophyta	2 (12%)	3 (16%)
Schizomycophyta	1 (6%)	1 (5%)

Summary of Periphyton Samples

Phylum	Control Pool Rocks Species Present	Test Pool Rocks Species Present
Chrysophyta	9 (75%)	7 (64%)
Cyanophyta	1 (8 %)	1 (9%)
Chlorophyta	2 (17%)	3 (27%)

Twelve of the nineteen species of organisms found in the phytoplankton were also found in the periphyton. The seven planktonic forms which did not appear in the periphyton were: Tabellaria flocculosa, Rhizosolenia eriensis, Melosira sp., Lyngbya contorta, Cylindrocapsa conferta and Sphaerotilus sp.

If the tabulations are examined further, and one considers each phylum by itself, it will be seen that twelve species of Chrystophytes were present in the plankton and that five of these were always found in the intake water and effluent water of both pools. A sixth species was present on every sampling date, excluding one. The organisms always present were: Nitzschia palea, Synedra sp., Achnanthes microcephala, Dinobryon cylindricum, and Rhizosolenia eriensis. On the same basis, it will be found that in the periphyton as well as in the phytoplankton the Chrysophytes constituted the important part of the growth. When periphyton organisms are listed by numerical rank as they were above, for the plankton, the arrangement is as follows: Nitzschia, Synedra, Achnanthes, Fragilaria capucina, Cymbella and

Gomphonema. The ranking used above relates only to the relative abundance of the organism within the phylum and not to its overall rank if all organisms are included. The comparative status of each species at each sampling site with regard to all the organisms counted is presented in Table 41.

It should be pointed out that Fragilaria, Cymbella and Gomphonema occurred with much greater frequency in the periphyton than in the phytoplankton. In the past (Putnam and Olson 1961), Cymbella and Gomphonema found in fish-net slimes from Lake Superior have been associated with extensive growths of these organisms on rocks along the North Shore. It was postulated that violent storms had broken portions of the periphyton masses loose and had swept them out into the lake where they then became entangled in the nets by the long gelatinous "stalks" which had served as the anchoring mechanism of the algae along the shore. All fishnet slimes examined by these investigators showed that a great part of the bulk of the slimes was made up of Cymbella and Gomphonema "stalks". At Castle Danger, while Cymbella and Gomphonema were regularly present in the periphyton they were not seen often in the plankton effluents from the pools. From Table 41 it will be seen that they ranked eleventh and sixteenth in the control pool and tenth and nineteenth in the test pool effluent. Apparently a very strong agitation of the water is needed to make these attached forms a part of the plankton and such velocities are never reached by the pool circulation.

Tables 36 through 40 reveal that Nitzschia, Synedra and Achnanthes not only are the most ubiquitous organisms present but also that they are the only forms which appear consistently in both the phytoplankton and periphyton samples at all sampling sites. Moreover it will be seen that in both periphyton and plankton the order of abundance at all points was always: Nitzschia, Synedra, Achnanthes. In his open lake studies of regrowth on artificially denuded rocks Fox (1969) noted that Synedra and Achnanthes were generally predominant and that in 1967 they were the only organisms found on all days and at all depths sampled.

The intake counts for both Nitzschia and Synedra were exceedingly high on the first sampling date (July 21) and remained, in fact, as the highest intake values recorded for each of these species. These particularly high values in the lakewater intake probably resulted from the effects of a rather severe "northeaster" which had occurred within this general area of Lake Superior on July 18 and 19 and which may have caused a detachment of many of the periphytic organisms from natural periphyton growths which characterize the rock Castle Danger shoreline. The total count of organisms in the incoming water decreased one full log cycle from 1,033,000 to 106,000 between July 21 and July 24. Counts in the influent water remained relatively low for the remainder of the season. Between August 4 and August 8 there was a dramatic drop in the temperature of the incoming lake water from 70° F to 43° F. This drop was accompanied by a corresponding decrease of the total phytoplankton count from approximately 380,000 to 62,000 organisms. This phenomenon probably represented a shift in the thermocline and the appearance of a new water mass in Lake Superior itself. Largely because of the exceedingly high value on July 21, the overall totals for the intake assign first place to Nitzschia while, actually, it was more abundant than Synedra on only three sampling dates. Achnanthes was always lowest of the three species in the intake data, except for July 24 when it ranked second.

If one wishes to test the hypothesis that periphyton can be an important source of organisms which typify the plankton perhaps the best approach is to deal with a single species because this approach is simpler and more readily understood than one which considers all forms at once. There is always a danger if results are averaged or "lumped" too greatly. We have already seen that in the experimental pools at Castle Danger Cymbella and Gomphonema species were not providing measurable additions to the plankton. This was explained on the basis that the violent water movements common in the lake itself did not exist in the sheltered pools. Also it is well known that the organisms mentioned are very firmly anchored. The alternative is clear. An organism typical to the periphyton which is not attached must be found, it must then be stimulated to the fullest growth possible in order to magnify any small tendencies it may have to join the plankton assembly. Thus if a given percentage is sloughed off one will, by increasing the number of individuals in the periphyton, increase the number of organisms leaving that community to become a part of the plankton. If this increase is sufficient to be detected by prevalent counting methods one has a device for checking periphyton contributions to the plankton.

Nitzschia palea is an organism suited to such a study and the test pools at Castle Danger provided the means for enrichment and growth stimulation. Nitzschia palea appears commonly as a benthic or littoral diatom and although definitely associated with the periphyton it is a motile form and is not attached. It is, furthermore, tolerant to certain types of fertilization. Its growth in oligotrophic waters should, therefore, be considerably enhanced by the addition of chemical nutrients. As the accompanying data show, this theory is amply substantiated by its spectacular growth on rocks in the nitrogen and phosphorus enriched test pool at Castle Danger. With a dosage of 0.163 ppm phosphate as PO_4-P and 1.96 ppm nitrate as NO_3-N, the growth of Nitzschia on rocks in the test pool was 2.9 times that found in the control pool. The foregoing figure is based on average results.

If proper allowance is to be made for the pools to come to full equilibrium a period of time should elapse before the first samples are taken. In this instance if the first two sampling periods are set aside as a type of "breaking in" period it will also eliminate any variations which might have been brought about by the "northeaster" and the high influent counts mentioned earlier. On this basis the time for experimental observation would include the period from July 30 to August 20th, or a time span of 2/3 of a month. Calculations made in accordance with this procedure indicated that the Nitzschia counts in the enriched pool were 2.7 times higher than in the control pool. This figure, though slightly lower than the first which was based on all samples is probably more trustworthy.

If one turns to the counts of Nitzschia palea found in the incoming water, the control pool effluent and the test pool effluent, and if the second method of calculation is adopted, the results are as follows:

Plankton Study 1970
Castle Danger Test Pools

Nitzschia palea Counts (Organisms/Liter)

Date	Influent water*	Effluent** Control Pool	Effluent** Test Pool
July 28	17,823	75,405	1,397,963
July 31	43,872	87,744	1,219,733
August 4***	10,968	10,054	65,351
August 8***	16,402	10,968	106,481
August 11	7,769	49,813	110,594
August 13	20,108	40,216	97,798
August 18	47,528	72,206	82,717
Average	23,496	49,486	440,091

* Water coming directly from Lake Superior
** Six overturns of water per day
*** Period characterized by sudden drop in temperature from 70°F (21°C) to 43°F (6°C)

It will be noted in the above tabulation that effluent waters were generally higher in organisms than the incoming water, in terms of Nitzschia palea cell counts. In the control pool the effluent counts were, on the average, only twice as high, and this might be considered as inconclusive evidence. However, in the enriched pool where Nitzschia growths on the rocks was luxuriant, there was an appreciable difference. On July 28th for example, the effluent contained 78 times as many N. palea cells as the influent. Three days later the difference was much less and the effluent count had dropped to 28 times that of the incoming water. On an average, the Nitzschia count was 18 to 19 times as great in the water leaving the test pool as in incoming waters. A difference of a log cycle can certainly be considered valid and on this basis the only explanation which fits the situation, especially since at six overturns a day water will remain in the pool for a period of four hours only, is that the "excess" Nitzschia palea observed in the effluent water was derived from the luxuriant periphyton growth observed on the bottom of the pool. This demonstrates that periphyton, under experimental conditions simulating a natural situation, can make contributions to the plankton and alter its composition.

Cyanophyta and Chlorophyta were only small contributors to the periphyton and plankton communities. Of the three Cyanophytes observed during this study, Oscillatoria was the only blue-green alga recorded from both the periphyton and the plankton. Lyngbya contorta and Coccochloris sp. were seen only in the plankton and were reported only once. Lyngbya was recorded in all plankton samples including the influent on August 4th. Similarly, Coccochloris was reported from all plankton samples on August 13th. Oscillatoria was found in the incoming lake water on one occasion only, namely August 4th. It was found in the control pool effluent on the same day in practically the same concentrations. During the remainder of the season it was found only in the test pool effluent where it was abundant during the whole period, July 31 to August 18.

In the periphyton samples, Oscillatoria was found only once in the control pool and this was on July 22 before the pools had been fully equilibrated. After that the periphyton samples from the control pool never had sufficiently high numbers of this species to be recorded. The enriched test pool on the other hand, in contrast to the control always had a good growth of Oscillatoria which constantly broke loose and floated away to become an important part of the plankton which characterized the effluent of this unit. Counts on the rocks in the test pool varied from 162,000 to more than five million cells per square centimeter. Correspondingly, while the influent samples of plankton were devoid of Oscillatoria (August 9th excepted), the test pool effluent after the periphyton growth matured, always contained this organism. The numbers found in the effluent varied from 95,000 to 1,400,000 per liter.

The growths of Oscillatoria sp. like those of Nitzschia palea demonstrated that the periphyton can be a source of plankton organisms and that it can greatly influence the composition of the plankton community.

Considering that the experimental program of this study was designed, in part, to assess the relationship of chemically enriched waters to algal abundance, it is assumed that the considerable difference in growth of Oscillatoria in the control and test pools is, at least partially if not largely, a function of the water quality in these two pools. Furthermore, its response to the enriched environment of the test pool as opposed to the basically oligotrophic waters of the control pool is consistent with the fact that this organism is a typical inhabitant of "polluted waters."

Chlamydomonas sp., Ulothrix zonata, Cylindrocapsa conferta, Scenedesmus sp. and Staurastrum sp. comprised the five Chlorophytes observed during the study period. Scenedesmus and Staurastrum were recorded for samples taken on August 19 only, and solely from the periphyton samples. Cylindrocapsa on the other hand was recorded for plankton samples only and was never listed for the periphyton. Ulothrix was observed once only in a plankton sample, but was recorded regularly from the periphyton where it was sufficiently abundant to rank fourth, just below Oscillatoria.

Unlike Ulothrix, the biflagellate vegetative cells of Chlamydomonas are highly motile and although it may often adhere to a substrate in its palmelloid stage it is usually not considered as being truly periphytic. At Castle Danger this organism was extraordinarily abundant as a member of the periphyton community of the test pool, where its numbers varied from roughly 700,000 to more than 3,000,000 per square square centimeter of rock surface. Like Nitzschia palea and Oscillatoria sp. the Chlamydomonas organisms became an important part of the test pool plankton after August 4th. Since this species did not come in with the influent water, in numbers which were detected by the counting procedure, its presence in the test pool effluent in concentrations ranging from approximately 500,000 to more than 2,000,000 organisms per liter is still another demonstration of the fact that the periphyton is a source of plankton organisms. During its four hour stay in the pool, at the temperatures which prevailed, it is not conceivable that so many organisms could have been produced in the supernatant water.

Summary and Conclusions

Nitzschia, Synedra, and Achnanthes appeared consistently in both the phytoplankton and in the periphyton at all sampling sites.

Nitzschia and Synedra counts were extremely high in intake water from Lake Superior, particularly following severe water movements and wave action in the lake.

On the average, Nitzschia palea counts were 18-19 time as great in water leaving the test pool as in incoming water.

The abundant growths of Oscillatoria in the test pool continually broke free to become part of the plankton community.

Fertilization of the test pool water produced a growth of Nitzschia palea 2.9 times greater than that found in the unfertilized control pool.

On the basis of the above observations it may be concluded that periphyton, particularly when it is very heavy in growth, does make a contribution to the plankton population of a lake.

TABLE 36

Lake Superior Plankton Counts [organisms/liter] — Castle Danger, Minn. (1970)

LAKEWATER INTAKE PIPE

Organism	Sampling Date									
	7/21	7/24	7/28	7/31	8/4	8/8	8/11	8/13	8/18	Total
CHRYSOPHYTA										
Achnanthes microcephala	20,108	15,995	10,511	26,506	11,425	3,199	5,941	10,511	29,248	133,444
Asterionella formosa	96,884	3,656	28,791	—	10,054	2,742	6,398	24,221	15,995	188,741
*Asterionella gracillima	—	—	—	13,253	—	—	—	—	—	13,253
Cymbella sp.	—	—	3,656	2,285	—	—	3,199	—	—	9,140
Dinobryon cylindricum	229,414	27,420	37,474	23,307	5,484	1,828	42,958	28,791	17,366	414,042
Fragilaria capucina	—	—	—	—	8,226	—	—	—	—	8,226
Gomphonema sp.	—	—	—	—	11,425	6,855	—	—	—	18,280
Nitzschia palea	573,078	10,968	17,823	43,872	10,968	16,402	7,769	20,108	47,528	748,516
Rhizosolenia eriensis	42,044	6,398	18,280	5,941	7,312	3,656	3,656	13,710	10,054	111,051
Synedra sp.	72,206	35,646	47,528	37,931	32,904	10,968	11,425	43,872	59,867	352,347
Tabellaria fenestrata	—	—	2,285	—	—	1,828	—	5,027	—	9,140
Tabellaria flocculosa	—	—	—	21,479	—	14,624	—	9,140	—	45,243
CYANOPHYTA										
Coccochloris sp.	—	—	—	—	—	—	—	41,587	—	41,587
Lyngbya contorta	—	—	—	—	89,115	—	—	—	—	89,115
Oscillatoria sp.	—	—	—	—	191,940	—	—	—	—	191,940
CHLOROPHYTA										
Chlamydomonas sp.	—	—	—	—	—	—	—	20,108	—	20,108
Cylindrocapsa conferta	—	—	—	—	—	—	67,179	22,393	44,329	133,901
SCHIZOMYCOPHYTA *Chlamydobacteriales*										
Sphaerotilus sp.	—	6,398	—	—	—	—	—	105,567	75,862	187,827
Total	1,033,734	106,481	166,348	174,574	378,853	62,102	148,525	345,035	300,249	

* Later re-identified and included with *A. formosa.*

TABLE 37

Lake Superior Plankton Counts [organisms/liter] — Castle Danger, Minn. (1970)

CONTROL POOL EFFLUENT

Organism	Sampling Date									
	7/21	7/24	7/28	7/31	8/4	8/8	8/11	8/13	8/18	Total
CHRYSOPHYTA										
Achnanthes microcephala	5,941	9,597	7,312	37,474	4,113	914	40,673	14,167	31,533	151,724
Asterionella formosa	17,366	10,511	23,764	16,452	8,226	7,312	3,656	16,452	13,710	117,449
Cymbella sp.	—	—	—	3,199	1,828	914	12,796	—	7,769	26,506
Dinobryon cylindricum	49,813	47,985	38,845	36,103	1,828	1,371	18,280	13,710	24,678	232,613
Fragilaria capucina	—	—	—	—	—	6,398	29,248	—	15,538	51,184
Gomphonema sp.	—	—	—	—	5,941	—	4,570	—	—	10,511
Nitzschia palea	68,550	308,932	75,405	87,744	10,054	10,968	49,813	40,216	72,206	723,888
Rhizosolenia eriensis	10,054	5,941	21,479	3,199	4,570	5,027	2,285	9,597	6,398	68,550
Synedra sp.	10,054	33,361	31,076	22,850	14,624	12,796	45,700	45,700	79,518	295,679
Tabellaria fenestrata	—	7,769	—	—	—	—	—	—	—	7,769
Tabellaria flocculosa	6,855	—	13,253	—	—	—	—	—	—	20,108
CYANOPHYTA										
Coccochloris sp.	—	—	—	—	—	—	—	11,882	—	11,882
Lyngbya contorta	—	—	—	—	26,506	—	—	—	—	26,506
Oscillatoria sp.	—	—	—	—	115,164	—	—	—	—	115,164
CHLOROPHYTA										
Chlamydomonas sp.	—	—	—	—	—	—	—	12,796	—	12,796
Cylindrocapsa conferta	—	—	—	—	—	—	62,152	—	—	62,152
SCHIZOMYCOPHYTA *Chlamydobacteriales*										
Sphaerotilus sp.	62,609	—	11,425	—	—	—	—	75,402	68,093	217,529
Total	231,242	424,096	222,559	207,021	192,854	45,700	269,173	239,922	319,443	

TABLE 38

Lake Superior Plankton Counts [organisms/liter] — Castle Danger, Minn. (1970)

TEST POOL EFFLUENT

Organism	Sampling Date									
	7/21	7/24	7/28	7/31	8/4	8/8	8/11	8/13	8/18	Total
CHRYSOPHYTA										
Achnanthes microcephala	10,511	14,167	13,253	19,651	3,656	3,656	18,280	10,511	21,479	115,164
Asterionella formosa	28,334	8,683	11,425	10,511	5,941	16,452	—	19,651	11,882	112,879
Cymbella sp.	—	3,199	—	—	—	—	—	—	—	3,199
Dinobryon cylindricum	86,373	54,840	37,017	15,995	4,113	16,909	23,764	14,167	19,651	272,829
Fragilaria capucina	—	—	—	—	—	—	—	—	4,570	4,570
Gomphonema sp.	—	—	—	47,528	15,538	13,710	32,447	—	—	109,223
Melosira sp.	—	—	—	—	5,027	11,425	—	—	—	16,452
Nitzschia palea	19,651	17,366	1,397,963	1,219,733	65,351	106,481	110,594	97,798	82,717	3,117,654
Rhizosolenia eriensis	12,796	24,678	15,081	2,742	2,742	14,167	4,570	12,339	7,312	96,427
Synedra sp.	15,538	53,012	29,705	16,909	17,823	25,135	19,194	48,899	53,469	279,684
Tabellaria fenestrata	—	2,742	—	2,742	—	—	—	—	—	5,484
Tabellaria flocculosa	6,855	2,742	2,742	—	—	—	—	—	—	12,339
CYANOPHYTA										
Coccochloris sp.	—	—	—	—	—	—	—	29,248	—	29,248
Lyngbya contorta	—	—	—	—	54,383	—	—	—	—	54,383
Oscillatoria sp.	—	—	—	369,256	95,056	264,603	1,423,098	1,022,309	439,177	3,613,499
CHLOROPHYTA										
Chlamydomonas sp.	—	—	—	—	—	2,435,810	542,916	704,694	456,086	4,139,506
Cylindrocapsa conferta	—	—	—	—	—	10,968	100,997	—	20,565	132,530
Ulothrix sp.	—	—	—	—	—	—	—	—	74,948	74,948
SCHIZOMYCOPHYTA *Chlamydobacteriales*										
Sphaerotilus sp.	103,285	—	—	—	—	56,668	—	88,658	58,039	306,650
Total	283,343	181,429	1,507,186	1,705,067	269,630	2,975,984	2,275,860	2,048,274	1,249,895	

TABLE 39

Lake Superior Periphyton, Rock Surface Growth [organisms/cm^2] — Castle Danger, Minn. (1970)

CONTROL POOL

Organism	Sampling Date					
	7/22	7/29	8/5	8/12	8/19	Total
CHRYSOPHYTA						
Achnanthes microcephala	671,396	584,577	540,523	707,381	665,838	3,169,715
Asterionella formosa	—	—	15,443	—	—	15,443
Cymbella sp.	114,768	135,450	—	141,475	224,526	616,219
Denticula sp.	—	64,160	—	—	—	64,160
Fragilaria capucina	149,199	78,419	772,177	41,263	224,526	1,265,584
Gomphonema sp.	86,076	121,193	72,069	70,737	38,711	388,786
Nitzschia palea	837,697	976,673	1,091,343	1,456,028	1,014,242	5,375,983
Synedra sp.	969,663	655,868	797,916	1,019,809	859,396	4,302,652
Tabellaria fenestrata	—	—	—	—	54,195	54,195
CYANOPHYTA						
Oscillatoria sp.	286,921	—	—	—	—	286,921
CHLOROPHYTA						
Chlamydomonas sp.	74,599	135,450	25,739	11,789	69,680	317,257
Staurastrum sp.	—	—	—	—	38,711	38,711
Total	3,190,319	2,751,790	3,315,210	3,448,482	3,189,825	

TABLE 40

Lake Superior Periphyton, Rock Surface Growth [organisms/cm^2] — Castle Danger, Minn. (1970)

TEST POOL

Organism	Sampling Date					
	7/22	7/29	8/5	8/12	8/19	Total
CHRYSOPHYTA						
Achnanthes microcephala	1,206,404	366,632	357,882	1,221,556	429,313	3,581,787
Cymbella sp.	116,743	141,012	92,585	325,392	—	675,732
Dinobryon cylindricum	45,400	—	—	—	—	45,400
Fragilaria capucina	—	401,886	405,249	592,108	922,229	2,321,472
Gomphonema sp.	116,743	—	126,311	335,236	—	578,290
Nitzschia palea	2,840,763	3,102,280	2,063,092	5,323,639	2,369,176	15,698,950
Synedra sp.	771,805	867,228	689,450	1,909,682	1,097,135	5,335,300
CYANOPHYTA						
Oscillatoria sp.	162,144	458,291	263,149	5,142,273	755,274	6,781,131
CHLOROPHYTA						
Chlamydomonas sp.	687,490	1,212,709	1,278,906	3,040,547	2,043,215	8,262,867
Scenedesmus sp.	—	—	—	—	166,954	166,954
Ulothrix sp.	—	91,658	784,184	4,326,123	636,020	5,837,985
Total	5,947,432	6,641,636	6,060,808	22,216,556	8,419,316	

TABLE 41

RANK OF PREDOMINANT ORGANISMS [PHYTOPLANKTON & PERIPHYTON]
Based on Count Totals During the Period: July 21 - August 19, 1970*
Lake Superior Limnological Study — Castle Danger, Minnesota (1970)

RANK	PHYTOPLANKTON			PERIPHYTON	
	LAKEWATER INTAKE *(17 species)*	CONTROL POOL EFFLUENT *(17 species)*	TEST POOL EFFLUENT *(19 species)*	CONTROL POOL ROCKS *(12 species)*	TEST POOL ROCKS *(11 species)*
1	Nitzschia palea	Nitzschia palea	∇ Chlamydomonas sp.	Nitzschia palea	Nitzschia palea
2	Dinobryon cylindricum	Synedra sp.	# Oscillatoria sp.	Synedra sp.	∇ Chlamydomonas sp.
3	Synedra sp.	Dinobryon cylindricum	Nitzschia palea	Achnanthes microcephala	# Oscillatoria sp.
4	Asterionella formosa	(Sphaerotilus sp.)	(Sphaerotilus sp.)	Fragilaria capucina	∇ Ulothrix sp.
5	# Oscillatoria sp.^{2}	Achnanthes microcephala	Synedra sp.	Cymbella sp.	Synedra sp.
6	(Sphaerotilus sp.)	Asterionella formosa	Dinobryon cylindricum	Gomphonema sp.	Achnanthes microcephala
7	∇ Cylindrocapsa conferta	# Oscillatoria sp.^{2}	∇ Cylindrocapsa conferta	∇ Chlamydomonas sp.	Fragilaria capucina
8	Achnanthes microcephala	Rhizosolenia eriensis	Achnanthes microcephala	# Oscillatoria sp.^{9}	Cymbella sp.
9	Rhizosolenia eriensis	∇ Cylindrocapsa conferta^{1}	Asterionella formosa	Denticula sp.^{7}	Gomphonema sp.
10	# Lyngbya contorta^{2}	Fragilaria capucina	Gomphonema sp.	Tabellaria fenestrata^{9}	∇ Scenedesmus sp.^{9}
11	Tabellaria flocculosa	Cymbella sp. + # Lyngbya contorta^{2}	Rhizosolenia eriensis	∇ Staurastrum sp.^{9}	Dinobryon cylindricum^{6}
12	# Coccochloris sp.^{4}	Tabellaria flocculosa	∇ Ulothrix sp.^{5}	Asterionella formosa^{8}	
13	∇ Chlamydomonas sp.^{4}	∇ Chlamydomonas sp.^{4}	# Lyngbya contorta^{2}		
14	Gomphonema sp.	# Coccochloris sp.^{4}	# Coccochloris sp.^{4}		
15	Cymbella sp. + Tabellaria fenestrata	Gomphonema sp.	Melosira sp.		
16	Fragilaria capucina^{2}	Tabellaria fenestrata^{1}	Tabellaria flocculosa		
17			Tabellaria fenestrata		
18			Fragilaria capucina^{5}		
19			Cymbella sp.^{1}		

* Phytoplankton totals based on 9 sampling days; periphyton totals based on 5 sampling days.

Cyanophyta (blue-green algae)
∇ Chlorophyta (green algae)
All other organisms are chrysophytes, except for *Sphaerotilus* (a filamentous bacterium).

Numerical superscripts: Indicate, as follows, those sampling dates on which the particular organism appeared only once among the predominant species counted: *1* = 7/24, *2* = 8/4, *3* = 8/11, *4* = 8/13, *5* = 8/18, *6* = 7/22, *7* = 7/29, *8* = 8/5, *9* = 8/19.

SECTION VIII

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Dr. Jackson L. Fox and Dr. Lee W. Stokes deserve special recognition for their painstaking work on photosynthetic pigments, primary productivity, taxonomy and general distribution of periphyton in the study areas of western Lake Superior.

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SECTION IX

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SECTION X

APPENDIX A

STATISTICAL PROCEDURES

The regression lines shown in the text were constructed using the least squares method as presented by Bancroft (1965). Procedures for determining correlation coefficients were derived from the same source. The coefficients (r) were calculated by use of the following formula:

$$r = \frac{n \sum XY - \sum X \sum Y}{\sqrt{n \sum X^2 - (\sum X)^2}\ \sqrt{n \sum Y^2 - (\sum Y)^2}}$$

In some cases, Y represents numbers of organisms and X represents chlorophyll concentration. In other correlations, Y represents photosynthetic rate, while X represents numbers of organisms. The lines were constructed to predict Y from X. The number of determinations (n) was seventeen for regular samples from 2.5, 5, 10, 15 and 20 feet. The n value for the thirty-five foot samples was sixteen. For the regrowth study, n was nine for the ten and twenty foot samples, and ten for the thirty-five foot samples. Probability values (P), which refer to the probability that r is different from zero, were determined from a correlation coefficient percentage point distribution table (Beyer, 1966).

In a general regression line, $Y - a + bX$, where a is the Y intercept and b is the slope. To determine b from the data, the following formula was used:

$$b_{yx} = \frac{n \sum XY - \sum X \sum Y}{n \sum X^2 - (\sum X)^2}$$

To determine the value of a, the calculated value of b is placed in the equation

$$Y = na + b \sum X$$

The calculated values of a and b are then inserted into the general formula $Y = a + bX$. A known value of X is inserted into the formula for the determination of the corresponding Y. The regression line is drawn through the calculated Y and the Y intercept.

APPENDIX B

SAMPLE CALCULATIONS

A. PIGMENT CONCENTRATIONS

Given:

Absorbance at 665 millimicrons = .345
645 = .122
630 = .099
510 = .111
480 = .356

Chl $\underline{a}$ (mg/L solvent) = $15.6D_{665} - 2.0D_{645} - 0.8D_{630}$;

$$\begin{array}{r} .345 \\ \text{x } 15.6 \\ \hline 5.382 \end{array} - \begin{array}{r} .122 \\ \text{x } 2 \\ \hline .244 \end{array} - \begin{array}{r} .099 \\ \text{x } .8 \\ \hline .792 \end{array} = \underline{4.346} \text{ mg Chl } \underline{a}\text{/L solvent}$$

Chl $\underline{b}$ (mg/L solvent) = $25.4D_{645} - 4.4D_{665} - 10.3D_{630}$;

$$\begin{array}{r} .122 \\ \text{x } 25.4 \\ \hline 3.0988 \end{array} - \begin{array}{r} .345 \\ \text{x } 4.4 \\ \hline 1.5180 \end{array} - \begin{array}{r} .099 \\ \text{x } 10.3 \\ \hline 1.0197 \end{array} = \underline{0.5611} \text{ mg Chl } \underline{b}\text{/L solvent}$$

Chl $\underline{c}$ (MSPU/L solvent) - $109D_{630} - 12.5D_{665} - 28.7D_{645}$;

$$\begin{array}{r} .099 \\ \text{x } 109 \\ \hline 10.7910 \end{array} - \begin{array}{r} .345 \\ \text{x } 12.5 \\ \hline 4.3125 \end{array} - \begin{array}{r} .122 \\ \text{x } 28.7 \\ \hline 3.5014 \end{array} = \underline{2.8771} \text{ MSPU Chl } \underline{c}\text{/L solvent}$$

$D_{res},510 = D_{510} - .0026C_a - .0035C_b - .0021C_c$;

$$D_{res},510 = .1110 - \begin{array}{r} 4.346 \\ \text{x}.0026 \\ \hline .0113 \end{array} - \begin{array}{r} .5611 \\ \text{x}.0035 \\ \hline .0196 \end{array} - \begin{array}{r} 2.8771 \\ \text{x }.0021 \\ \hline .0060 \end{array} = \underline{.0741}$$

$D_{res},480 = D_{480} - .0019C_a - .0136C_b - .0054C_c$;

$$D_{res},480 = .3560 - \begin{array}{r} 4.346 \\ \text{x}.0019 \\ \hline .0082 \end{array} - \begin{array}{r} .5611 \\ \text{x}.0136 \\ \hline .0076 \end{array} - \begin{array}{r} 2.8771 \\ \text{x}.0054 \\ \hline .0011 \end{array} = \underline{.3391}$$

Ast. Car. (MSPU/L solvent) = $2(4.45D_{res},510 - D_{res},480)$

$$\begin{array}{r} .0741 \\ \underline{\times\ 4.45} \\ .329 \end{array} - .3391 \times 2 = \underline{0} \text{ MSPU Ast. Car./L solvent}$$

Non-ast. Car. (MSPU/L solvent) =

$$7.6\ (D_{res},480 - 1.49D_{res},510)$$

$$.3391 - \begin{array}{r} .0741 \\ \underline{\times\ 1.49} \\ .1034 \end{array} \times 7.6 = 1.7913 \text{ MSPU Non-ast. Car./L solvent}$$

$$\text{Mg (MSPU) pigment/L solvent} \times \frac{\text{L solvent}}{1000} \times \frac{\text{L sample}}{\text{L aliquot}}$$

$$\times \frac{100}{\text{cm}^2 \text{ rock surface}} = \text{Mg (MSPU) pigment/100 cm}^2 \text{ rock surface}$$

B. Q_{10} CALCULATION

Given:

Photosynthetic rate at 10° C = 12.6 microliters O_2 per mg ash-free dry weight

Photosynthetic rate at 15° C = 16.4 microliters O_2 per mg ash-free dry weight

$Q_{10} = (p_2/p_1)^{10/t_2-t_1}$

$Q_{10} = (16.4/12.6)^{10/15-10}$

$Q_{10} = (1.3)^2$

$Q_{10} = \underline{1.69}$ for the temperature range 10-15°

APPENDIX C

LAKE SUPERIOR STUDIES
CHECKLIST OF PERIPHYTON ORGANISMS*

SUMMER 1970

Phylum Chrysophyta

- Class Bacillariophyceae
  - *Achnanthes lanceolata* (Brebisson) Grunow
  - *Achnanthes microcephala* (Kuetzing) Cleve
  - *Amphiprora ornata* Bailey
  - *Amphora ovalis* Kuetzing
  - *Asterionella formosa* Hassall
  - *Ceratoneis arcus* (Ehrenberg) Kuetzing
  - *Cocconeis* group:
    - *C. flexella* (Kuetzing) Cleve
    - *C. pediculus* Ehrenberg
    - *C. placentula* Ehrenberg
  - *Cyclotella antiqua* Wm. Smith
  - *Cyclotella bodanica* Eulenstein
  - *Cymatopleura solea* (Brebisson) Wm. Smith
  - *Cymbella* group:
    - *C. cistula* (Hemprich) Grunow
    - *C. lanceolata* (Ehrenberg) Van Heurck
    - *C. leptoceros* (Ehrenberg) Grunow
    - *C. parva* (Wm. Smith) Cleve
    - *C. prostrata* (Berkeley) Cleve
    - *C. ventricosa* Kuetzing
  - *Denticula thermalis* Kuetzing
  - *Diatoma hiemale* (Lyngbye) Heiberg
  - *Diatoma vulgare* Bory
  - *Diploneis puella* (Schuman) Cleve
  - *Epithemia turgida* (Ehrenberg) Kuetzing
  - *Eunotia monodan Ehrenberg* var. *major* (Wm. Smith) Hustedt
  - *Eunotia pectinalis* (Kuetzing) Rabenhorst var. *minor* (Kuetzing) Rabenhorst
  - *Fragilaria capucina* Desmazieres
  - *Fragilaria crotenensis* Kitton
  - *Frustulia viridula* (Brebisson) Detoni
  - *Gomphoneis herculeana* (Ehrenberg) Cleve
  - *Gomphonema* group:
    - *G. angustatum* var. *obtusatum* (Kuetzing) Van Heurck
    - *G. constrictum* Ehrenberg
    - *G. geminatum* (Lyngbye) C. A. Agardh
    - *G. gracile* Ehrenberg var. *dicotoma* (Kuetzing) Grunow

---

* Based on studies of the near-shore areas of Lake Superior's North Shore and the Castle Danger Control Pool.

  - *G. olivaceum* (Lyngbye) Kuetzing
  - *G. olivaceum* var. *calcarea* Cleve
- *Melosira granulata* (Ehrenberg) Ralfs
- *Melosira varians* C. A. Agardh
- *Navicula* group:
  - *N. dicephala* (Ehrenberg) Wm Smith
  - *N. dicephala* var. *elginensis* (Gregory) Cleve
  - *N. oblonga* Kuetzing
  - *N. pupula* Kuetzing
  - *N. radiosa* Kuetzing
  - *N. reinhardtii* (Grunow) Van Heurck
  - *N. tuscula* Ehrenberg
- *Nitzschia* group:
  - *N. denticula* Grunow
  - *N. dissipata* (Kuetzing) Grunow
  - *N. hungarica* Grunow
  - *N. linearis* (Agardh) Wm. Smith
  - *N. palea* (Kuetzing) Wm. Smith
  - *N. vermicularis* (Kuetzing) Hatzsch
- *Pinnularia* group:
  - *P. cardinalis* (Ehrenberg) Wm. Smith
  - *P. major* (Kuetzing) Wm. Smith
  - *P. viridis* (Nitzsch) Ehrenberg
- *Rhizosolenia eriensis* H. L. Smith
- *Rhoicosphenia curvata* (Kuetzing) Grunow
- *Stauroneis anceps* Ehrenberg var. *anceps*
- *Stauroneis obtusa* Lagerst
- *Stephanodiscus* sp.
- *Surirella angusta* Kuetzing
- *Surirella linearis* Wm. Smith
- *Surirella* sp.
- *Synedra* group:
  - *S. acus* Kuetzing
  - *S. rumpens* Kuetzing
  - *S. ulna* (Nitzsch) Ehrenberg
- *Tabellaria fenestrata* (Lyngbye) Kuetzing
- *Tabellaria flocculosa* (Roth) Kuetzing

Class Chrysophyceae

- *Dinobryon sertularia* Ehrenberg
- *Dinobryon* sp.

Phylum Chlorophyta

- *Chlamydomonas* spp.
- *Cosmarium* sp.
- *Mougeotia* sp.
- *Oedogonium* sp.
- *Pediastrum duplex* Meyen
- *Pithophora* sp.

Scenedesmus obliquus (Turpin) Kuetzing
Scenedesmus quadricauda (Turpin) Brebisson
Schizomeris leibleinii Kuetzing
Selenastrum sp.
Staurastrum sp.
Ulothrix tenerrima Kuetzing
Ulothrix zonata (Weber & Mohr) Kuetzing
Stigeoclonium subsecuntum Kuetzing

Phylum Cyanophyta
Aphanothece microspora (Menegh) Rabenhorst
Chroococcus minor (Kuetzing) Naegeli
Lyngbya martensiana var. *calcarea* Tilden
Merismopedia convoluta Brebisson
Oscillatoria tenuis C. A. Agardh
Oscillatoria sp.
Plectonema wollei Farlow

Appendix D

Publications of Research Supported in Part by EPA Project 18050 DBM

Adess, Michael L., Nelson, Robert R., Schlottman, Loren L. and Parkos, William G. 1971. A study of the potential of periphyton organisms as components of Lake Superior plankton. Limresta Bulletin, Lake Superior Research Station, Duluth, Minn. Research Report No. 2.

Fox, J. L., T. A. Olson and T. O. Odlaug. 1967. The collection, identification, and quantitation of epilithic periphyton in Lake Superior. Proc., 10th Conf. on Great Lakes Res.; International Assoc. for Gt. Lakes Res., Ann Arbor, Michigan. pp. 12-19.

Fox, J. L. 1969. The epilithic periphyton of the western arm of Lake Superior. Ph.D. thesis, Univ. of Minnesota. 243 pp.

Fox, Jackson L,, T. O. Odlaug, and T. A. Olson. 1969. The ecology of periphyton in western Lake Superior. Part I: Taxonomy and distribution. Bulletin 14, Water Resources Research Center, Minneapolis, Minnesota. 127 pp.

Stokes, L. W., T. A. Olson, and T. O. Odlaug. 1967. Studies of Chlorophyll and Carotenoid Pigments in Lake Superior Periphyton. Proc., 10th Conf. on Grt. Lakes Res., International Association for Great Lakes Research, p. 107-114, Ann Arbor, Michigan.

Stokes, L. W. 1969. The productivity of Lake Superior periphyton as reflected by pigment analysis and respirometry. Ph.D. thesis. 313 pp.

Stokes, L. W., T. A. Olson, and T. O. Odlaug. 1970. The photosynthetic pigments of Lake Superior periphyton and their relation to primary productivity. Bulletin no. 18. Water Resources Research Center University of Minnesota. 150 pp.

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27 Abstract
Laboratory and field studies were conducted to evaluate the importance of periphyton in western Lake Superior with special reference to the make-up and distribution of the periphyton growths and to the overall importance of productive capacity of this assemblage of organisms. The taxonomic portion of the investigation indicated that over 90% of the total number of organisms were diatoms and that the phyla to which these diatoms belonged were the Chrysophyta, the Chlorophyta, and the Cyanophyta. Predominant genera were Synedra, Achnanthes, Navicula, Cymbella, and Gomphonema. In many respects, the periphyton of Lake Superior was similar to that found in streams and there was evidence that the interrelated factors that affected periphyton growths were temperature, light intensity, depth of water, water movements, nutrient levels, and the type of substrate. Artificially denuded rocks demonstrated definite re-growth but after 46 days this growth level was only 18% of that occurring naturally. The mean total counts of organisms in the primary sampling area ranged from 497,000 to 1,470,000 per square centimeter of rock surface. Studies of the pigment concentrations showed that the biomass of periphyton along the North Shore of Lake Superior resemble those of other oligotrophic bodies of water and range from 0.338 to 3.59 mg of total pigment per 100 square centimeters of rock surface. The average was 1.36 mg per 100 square centimeters of rock surface. Pigment ratios indicated that the Lake Superior periphyton was dominated by the Chrysophyta.

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Abstract (continued)

Assimilation values for Stony Point Bay averaged 1.48 grams of carbon fixed per gram of chlorophyll in 1967. In Stony Point Bay, the total standing crop in terms of dry weight was 55.5 tons. In re-growth studies, chlorophyll levels were observed to increase by an average of 0.057 grams (57 mgs) per square meter per day. The efficiency of energy utilization in Stony Point Bay was found to be 0.082%, a typical value for algal communities.

(T.O. Olson and T. O. Odlaug) University of Minnesota

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